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# Bryozoa from the Lower Carboniferous (Viséan) of County Fermanagh, Ireland

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## CONTENTS

**Synopsis.** A systematic appraisal of the partially silicified Lower Carboniferous bryozoan fauna of County Fermanagh has demonstrated a rich and diverse bryozoan fauna of which the fenestrate portion has been largely described earlier by other authors. This paper describes the remaining cryptostome, trepostome, and cystoporate elements of the fauna, as well as a few previously ignored fenestrate taxa.

24 species are described (9 cryptostome species; 6 fenestrate species; 6 trepostome species; and 3 cystoporate species) of which 6 are new species and 2 new combinations. The new species are the arthrostylid cryptostomes *Hexites paradoxus, Nematopora hibernica,* and *Pseudonematopora planatus,* the rhomboporid cryptostomes *Rhombopora cylindrica,* and *Rhombopora hexagona,* and the trepostome *Leioclema indentata*. The new combinations are *Clausotrypa ramosa* (Owen), and *Rhombocladia dichotoma* (M'Coy). For completeness brief descriptions are given of the following taxa, which have been described more fully elsewhere: *Rhabdomeson progracile* Wyse Jackson & Bancroft, *Baculopora megastoma* (M'Coy), *Diploporaria tenella* Wyse Jackson, *Thamniscus colei* Wyse Jackson, and *Fistulipora incrustans* (Phillips, 1836).

The genus *Leioclema* and the species *Streblotrypa pectinata* Owen, *Diploporaria marginalis* (Young & Young), *Dyscritella miliaria* (Nicholson), *Tabulipora howsii* (Nicholson), and *Tabulipora minima* Lee are reported from Ireland for the first time. The following genera are reported from the British Isles for the first time: *Hexites, Pseudonematopora* and *Clausotrypa*. Lectotypes are designated for *Diploporaria marginalis* (Young & Young), *Ichthyorachis newenhami* M'Coy, *Rhombocladia dichotoma* (M'Coy), *Dyscritella miliaria* (Nicholson), *Tabulipora howsii* (Nicholson), and *Tabulipora minima* Lee. Nomenclature problems for several species have been clarified. A tabular and dichotomous key is given for the complete fauna (including taxa described earlier by other authors). Patterns of silicification show that replacement of calcified bryozoan zoaria by silica was delayed.

## INTRODUCTION

Bryozoans comprise a significant component of Lower Carboniferous faunal assemblages in Ireland. However, they are often fragmentary in nature which has made them difficult to study. Nevertheless, Lower Carboniferous bryozoans have been the subject of research since the mid-1800s when M'Coy (1844) described many species. In the last thirty years recent studies (Miller 1961a, 1961b, 1962a, 1962b, 1963, Owen 1973, Tavener-Smith 1973, Olaloye 1974, Bancroft 1985, 1986b, Bancroft & Wyse Jackson 1995, Wyse Jackson 1988, Wyse Jackson & Bancroft 1995a) have resulted in the description of new taxa, the redescription of previously described taxa, and give detailed quantitative and statistical analysis of these taxa. While these studies have increased the biostratigraphical value of Carboniferous bryozoans from Ireland, there is still considerable work to be carried out to assess faunas of particular Brigantian stages.

This present study adds to the taxonomic diversity of bryozoans described from Ireland, and shows some similarities at generic level, to Lower Carboniferous faunas of the Russian Platform. This paper describes 24 bryozoan species of Lower Carboniferous (Viséan, Asbian) age from County Fermanagh, Ireland. An unusual nodular trepostome and a species of the cystoporate genus *Goniocladia*, that exhibits atypical branching patterns will be described elsewhere.

## PREVIOUS WORK

The largely silicified fauna from County Fermanagh, dominated by bryozoans and brachiopods, has been the subject of several papers: Tavener-Smith (1965a) erected the genus *Ptilofenestella*, described a species of *Minilya* (1965b, 1981), noted the occurrence of ovicells in *Fenestella* (1966), described a new species of *Polypora* (1971), and monographed 32 species from eight genera of which three were new (1973). Olaloye (1974) examined the acanthocladiid element, describing nine species of *Penniretepora*, five being new. Three new fenestrate taxa that were discovered in the Carrick Lough fauna during the present study have been described elsewhere (Wyse Jackson 1988), and two species of the cryptostome genus *Rhabdomeson* and the cystoporate taxon *Fistulipora incrustans* (Phillips, 1836) are described more fully by Wyse Jackson & Bancroft (1995a), and Bancroft & Wyse Jackson (1995).

## MATERIAL

The bryozoans described in this study were collected at two localities, Carrick Lough and Sillees River (Fig. 1) from thin beds of pale grey and muddy limestones that have been assigned to the upper part of the Glencar Limestone (Brunton & Mason 1979, George *et al.* 1976) (Fig. 2). Nearly 50 kg of rock from Carrick Lough containing both silicified and calcified bryozoan zoaria was processed, and additionally many thousands of unsorted etched silicified specimens (from the Brunton and Tavener-Smith collections in the Natural History Museum) and a small number of limestone blocks (from the Mason collection in the Ulster Museum) were examined. A small number of silicified specimens extracted from limestone collected from drift deposits close to Lough Gara, County Roscommon were also included in this study.

Silicified bryozoan colonies were acid-etched from the surrounding limestones. Calcified bryozoan zoaria were extracted from the muddy limestone using the surfactant 'Quaternary O'. Specimens were then sorted by taxon and stored in cavity slides. Thin section and acetate peels were produced to examine the internal features of the bryozoans.

Type and other material from the Griffith Collection in the National Museum of Ireland, the Owen Collections in the Manchester (prefix LL) and Ulster Museums, the Vine Collection in the National Museum of Wales, Cardiff (prefix NMW), the Nicholson Collection in Aberdeen University (prefix AUGD), the National Museum of Scotland, Edinburgh (prefix RSM), the Whidborne and Porter Collections in the Sedgwick Museum, Cambridge (prefix SMC), and the Phillips Collection in the British Geological Survey Keyworth (prefix BSG) was referred to for comparison with the

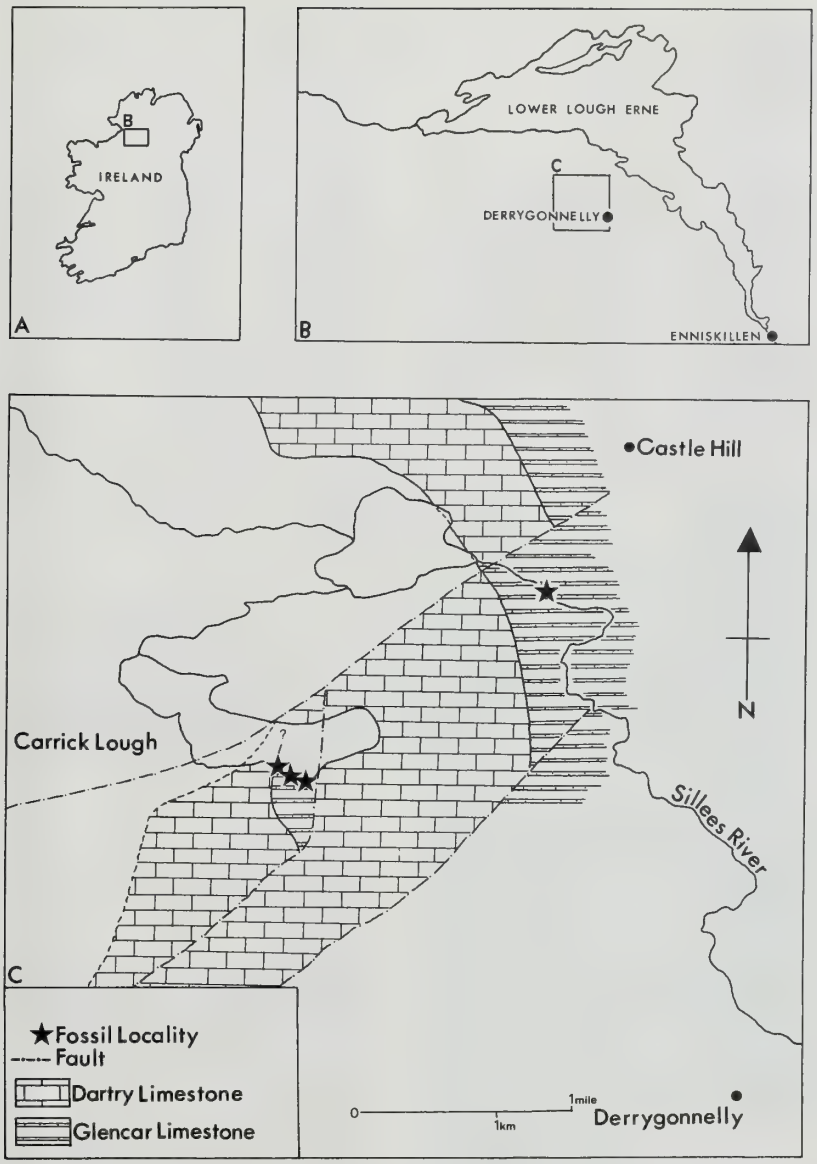



Fig. 1 Location map showing the collecting localities at Carrick Lough and Sillees River, County Fermanagh, Ireland.

tudy material. A number of taxa from these collections have been eassigned and redescribed in the light of taxonomic work carried ut on the County Fermanagh fauna.

Specimens have been deposited in a number of museums. The argest collection is lodged in the Natural History Museum, London prefix BMNH PD). A voucher collection which includes some aratype material has been lodged in the Geological Museum, Trinity College Dublin (prefix TCD.). In addition some paratypes of number of fenestrates (see Wyse Jackson 1988) have been deposted in the National Museum of Ireland (prefix NMING:F) and the Ulster Museum (prefix BELUM K).

Morphometric measurements for every taxon were taken on at east 12 specimens, if available, and up to ten measurements were nade on each parameter on each specimen, using a Leitz binocular nicroscope fitted with a linear graticule at magnifications of between ×40 and ×100. The mean, standard deviation, and intracolonial and intercolonial coefficients of variation were computed and are tabulated within the description of each taxon. Abbreviations used in these tables are: CV = Coefficient of Variation; CVw = Intra (within) Colonial Variation; CVb = Inter (between) Colonial Variation; NM = Number of measurements; Mn = Minimum value recorded; Mx = Maximum value recorded; x = Mean value; N = Number of specimens measured; explanations for other abbreviations used are given in Figs 3, 18, 42, 59 and 84.

The measurement scheme for cryptostomes is modified from Newton (1971) (Figs 3, 18); for fenestrates from Tavener-Smith (1973) (Fig. 42); for trepostomes from Boardman (1960) and Cuffey (1967) (Fig. 59); and for cystoporates from Warner & Cuffey (1973) (Fig. 84).

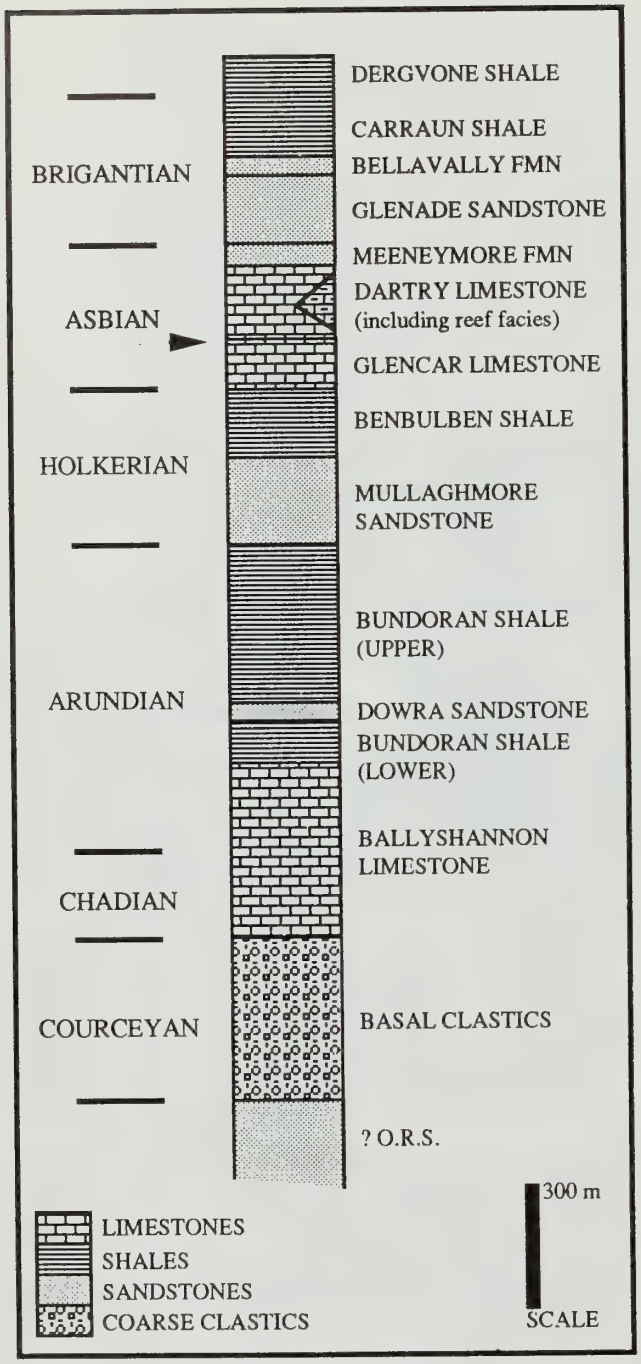



**Fig. 2** Stratigraphical succession in west County Fermanagh. Bryozoan horizon at the top of the Glencar Limestone arrowed.

## SYSTEMATIC PALAEONTOLOGY

During the course of this study three cases of misidentification of taxa in earlier described collections came to light. All cases have a bearing on the systematics of the Asbian bryozoan fauna described below. The first two cases of misidentification were those of M'Coy (1844) who identified two Lower Carboniferous bryozoans as being conspecific with two Devonian taxa (*Millepora gracilis* and *Millepora similis*) described three years earlier by Phillips (1841). The Carboniferous taxa have been redescribed and named, below and elsewhere (Wyse Jackson & Bancroft, 1995a) as *Rhombopora cylindrica* sp. nov. and *Rhabdomeson progracile* respectively. *Millepora gracilis* as originally described by Phillips (1841) contains specimens herein considered to belong to two genera – *Rhabdomeson* and *Rhombopora*. The third case of misidentification is that of Owen (1966). *Rhombopora radialis* Owen, 1966 is synonomised with *Pseudonematopora turkestanica* (Nikiforova, 1948). More detailed discussion of the contrasting taxa is given in the discussion section of *Pseudonematopora planatus* sp. nov. and *Rhombopora cylindrica* sp. nov., and in Wyse Jackson & Bancroft (1995a)

For completeness brief descriptions are given of the following taxa which have been described more fully elsewhere: *Rhabdomeson progracile* Wyse Jackson & Bancroft 1995, *Rhabdomeson rhombiferum* (Phillips, 1841), *Baculopora megastoma* (M'Coy, 1844), *Diploporaria tenella* Wyse Jackson, 1988, *Thamniscus colei* Wyse Jackson, 1988, and *Fistulipora incrustans* (Phillips, 1836).

Phylum **BRYOZOA** Ehrenberg, 1831
Class **STENOLAEMATA** Borg, 1926
Order **CRYPTOSTOMATA** Vine, 1884a
Suborder **RHABDOMESINA** Astrova & Morozova, 1956
Family **ARTHROSTYLIDAE** Ulrich, 1882
Genus ***HEXITES*** Shulga-Nesterenko, 1955

TYPE SPECIES. *Hexites triangularis* Shulga-Nesterenko, 1955 by monotypy from the Lower Carboniferous of Chekhurskiv in the Russian Platform.

EMENDED DIAGNOSIS. Arthrostylid with dendroid, erect zoaria composed of small delicate branches, with polygonal cross-sections. Perpendicular lateral branches occasionally developed. Jointing unknown. Autozooecial apertures oval to elliptical in shape, arranged in five to eight longitudinal rows and separated by a distinct ridge. Autozooecial chambers triangular to sub-triangular in cross-section. Zooecia seven to ten times longer than wide, diverging at a low angle with slightly inflated bases and sublinear chambers. Hemisepta and diaphragms not present. Small acanthostyles frequently developed on ridges.

DISCUSSION. The genus *Hexites* Shulga-Nesterenko 1955 was erected for distinctive small dendroid six-sided arthrostylids. Later, Dunaeva (1974: 93) included the eight-sided variety *Hexites quadrangularis*. The taxon from County Fermanagh described here has very similar morphological features to that of *Hexites triangularis* but differs from it in that as many as eight longitudinal rows may be developed. It might be acceptable to erect a new genus to incorporate *H. quadrangularis* and the Irish form but is probably taxonomically unnecessary; rather the diagnosis of *Hexites* has been emended here to include all three taxa.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Viséan).

DISTRIBUTION. Only known from Ireland and the CIS (former Soviet Union).

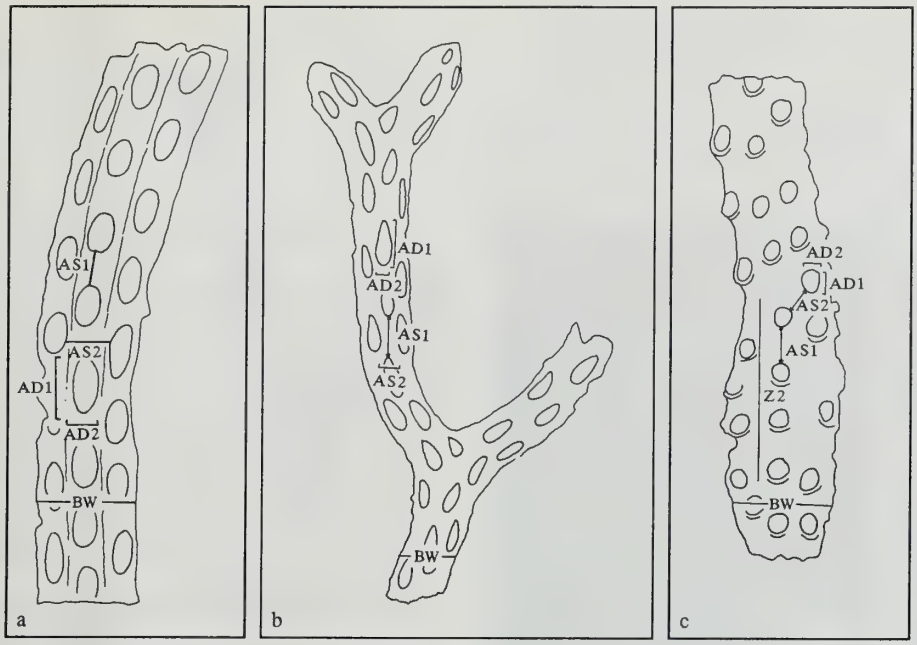



**Fig. 3** Measurements taken on arthrostylid cryptostomes in this study. **a**, *Hexies paradoxus* sp. nov.; **b**, *Nematopora hibernica* sp. nov.; **c**, *Pseudonematopora planatus* sp. nov. BW = Branch diameter; AD1 = Autozooecia apertural diameter measured parallel to growth direction; AD2 = Autozooecia apertural diameter measured perpendicular to growth direction; AS1 = Autozooecia apertural spacing measured parallel to growth direction; AS2 = Autozooecia apertural spacing measured perpendicular to growth direction; AR = Number of longitudinal apertural rows around zoarium; Z2 = Number of autozooecial apertures contained within a 2mm line measured parallel to growth direction.

***Hexites paradoxus*** sp. nov. Figs 3a, 4–5, 8

HOLOTYPE. BMNH PD9410; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

PARATYPES. BMNH PD9411-9429; TCD.34012-34014, 34125, 34127, 34164, 34167, 42593c, all from the same locality and horizon as the holotype. TCD.42514-42515, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DERIVATION OF TRIVIAL NAME. This *Hexites* species has between five and eight rows of autozooecial apertures, unlike the type species which has six, so therefore is a paradox.

DIAGNOSIS. *Hexites* with a delicate dendroid zoarium. Branches are straight to gently curved with a polygonal to sub-polygonal cross-section. Lateral branches diverge nearly perpendicular to the main stem and are infrequently developed. Autozooecia developed in five to eight longitudinal rows around the complete branch. The reverse surface is seen only as a very thin groove. Autozooecial apertures are small, oval to elliptical in shape. Apertural rows are divided by sharp distinct longitudinal ridges. Stylets developed on ridges and occasionally between successive autozooecial apertures.

DESCRIPTION. Colonies are small, delicate, and dendroid. Branches are straight and of constant diameter along their length. Branch cross-sections are polygonal to rarely sub-polygonal. Lateral branches of a similar diameter diverge at unknown intervals perpendicular to the main branch. There is a very slight increase in branch width at bifurcations. The largest fragment examined measured 9.8 mm in length.

Autozooecia are developed in five to eight longitudinal rows around most of the branch. In some specimens the reverse surface is represented by a thin groove (Fig. 5). Autozooecia arise from a thin central axis and diverge from it a low angle. Chamber bases are slightly inflated. Chambers are sublinear in shape, 0.60 to 0.71 mm in length and at least ten times as long as wide. In cross-section they are triangular to polygonal in shape. The vestibule, which shallows distally, is orientated at an angle of between 45° and 60° to the zoarial surface. The distal wall is thin with slight thickening of the proximal frontal wall. Hemisepta and diaphragms are not present.

Autozooecial apertures (0.28 × 0.14mm) occur in longitudinal rows that are separated by a sharp to rounded ridge 0.08 mm wide. They are oval to elliptical in shape, and occasionally narrow distally. They are regularly spaced one diameter apart within rows and one to two diameters apart between rows. Autozooecial aperture size is marginally greater and apertural spacing slightly less in those rows closest to the groove on the reverse of branches.

One to two rows of small short acanthostyles 0.02mm wide occur on the crest of ridges. Interapertural areas may be smooth or be decorated with up to twelve acanthostyles in three rows.

**Table 1** Measurements of *Hexites paradoxus* (in mm). N=18.

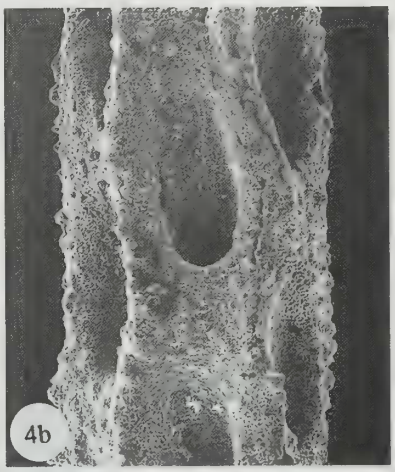
| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW | 136 | 0.59 | 0.37 | 0.72 | 3.73 | 8.43 |
| AD1 | 152 | 0.28 | 0.20 | 0.43 | 10.55 | 7.00 |
| AD2 | 157 | 0.14 | 0.08 | 0.22 | 10.88 | 6.64 |
| AS1 | 142 | 0.22 | 0.09 | 0.42 | 14.08 | 4.78 |
| AS2 | 158 | 0.26 | 0.13 | 0.40 | 14.81 | 7.31 |

DISCUSSION. *Hexites* is easily recognised by the arrangement of autozooecia in well-developed longitudinal rows, with strong interapertural ridges.

**Table 2** Quantitative comparison between Carboniferous *Hexites* species (dimensions in mm).

| | AR | BW | AD1 | AD2 | AS1 | AS2 |
|---|---|---|---|---|---|---|
| *H. paradoxus* sp. nov. | 5–8 | 0.37–0.72 | 0.20–0.43 | 0.08–0.22 | 0.09–0.42 | 0.13–0.40 |
| *H. triangularis* Shulga-Nesterenko, 1955 | 6 | 0.18–0.38 | 0.17 | 0.08 | – | – |
| *H. quadrangularis* Dunaeva, 1974 | 8 | 0.52 | 0.16 | 0.12 | 0.18 | 0.15 |

Data from original sources.






## Genus *NEMATOPORA* Ulrich, 1888a

*H. paradoxus* is only the third *Hexites* species to be described and first outside of the CIS (former Soviet Union). It differs from the type species *H. triangularis* Shulga-Nesterenko 1955 in having a larger branch width, a variable number of autozooecial rows (five to eight and not the consistent six of the latter), no peristomes, and acanthostyles in interapertural areas. It bears a close resemblance to *H. quadrangularis* Dunaeva 1974, which has 8 rows of autozooecia. However, *H. paradoxus* shows some morphological differences: branches are often thicker, autozooecial apertures are larger, elliptical to oval in shape, and are spaced considerably further apart. On the basis of these morphological differences *H. paradoxus* is erected as a new species (Table 2).

STRATIGRAPHICAL RANGE. Lower Carboniferous (Viséan–Asbian).

DISTRIBUTION. Carrick Lough and Sillees River, County Fermanagh, Ireland.

TYPE SPECIES. *Trematopora minuta* Hall, 1876 by original designation, from the middle Silurian of Waldron, Indiana, U.S.A.

REVISED DIAGNOSIS. Arthrostylid with delicate, erect, dichotomously branching zoarium. Branches straight, circular to sub-circular in cross-section. Autozooecia arranged in four to ten longitudinal rows, either completely around branches or concentrated on one side of branch. Interapertural areas smooth with acanthostyles developed along ridges. Autozooecial apertures are oval to rhombic, dorsally flared.

STRATIGRAPHICAL RANGE. Middle Ordovician–Lower Permian.

DISTRIBUTION. British Isles, Europe, North America, the CIS (former Soviet Union), Asia.

***Nematopora hibernica*** sp. nov. Figs 3b, 6–7, 9

HOLOTYPE. BMNH PD9430; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

**Figs 4–5** *Hexites paradoxus* sp. nov. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. **4**, BMNH PD9410 **(holotype)**; **4a**, colony fragment comprising a thin slender octagonal to circular-shaped branch; autozooecia are arranged in distinct longitudinal rows divided by strong flexous ridges, and their apertures are oval in shape, ×30; **4b**, detail of 4a showing autozooecial apertures and intervening ridges showing the disposition of small stylets on the crest of ridges, ×150. **5**, BMNH PD9414 (paratype), reverse surface showing longitudinal groove, ×12.

**Figs 6, 7** *Nematopora hibernica* sp. nov. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. **6**, BMNH PD9430 **(holotype)**; **6a**, small colony fragment showing bifurcation of branches, and regular arrangement of autozooecial apertures in offset rows on obverse surface, ×20; **6b**, detail showing distal growing tip of branch and pyriform autozooecial apertures separated by thin interapertural walls patterned by a single row of small stylets, ×120. **7**, BMNH PD9442 (paratype), reverse surface showing longitudinal rows of small nodes, ×14.

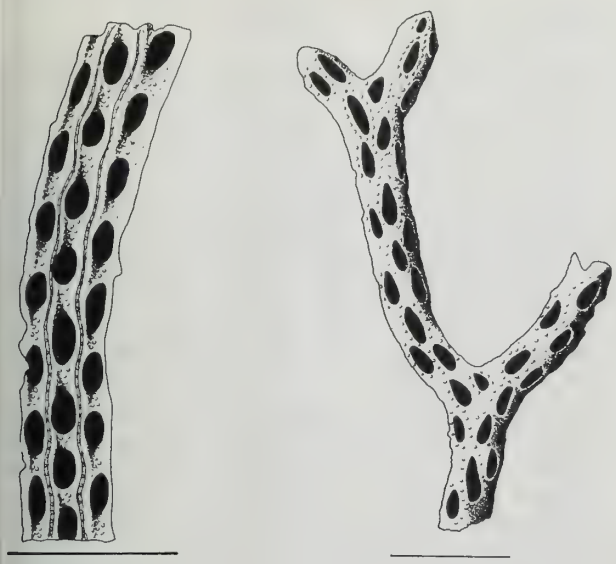


**Fig. 8** *Hexites paradoxus* sp. nov. Line drawing of external features of BMNH PD9410; scale bar = 1 mm.

**Fig. 9** *Nematopora hibernica* sp. nov. Line drawing of external features of BMNH PD9430); scale bar = 1 mm.

PARATYPES. BMNH PD9431-9449; TCD.34015-34017; BELUM K3145-3146; all from the same locality and horizon as the holotype.

DERIVATION OF TRIVIAL NAME. From the Latin *hibernica* meaning reland.

**Table 3** Measurements of *Nematopora hibernica* (in mm). N=19.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW | 176 | 0.59 | 0.41 | 0.76 | 7.99 | 9.81 |
| AD1 | 176 | 0.33 | 0.21 | 0.44 | 8.63 | 9.84 |
| AD2 | 172 | 0.12 | 0.08 | 0.20 | 10.34 | 6.89 |
| AS1 | 165 | 0.27 | 0.11 | 0.52 | 22.04 | 6.04 |
| AS2 | 170 | 0.12 | 0.08 | 0.21 | 17.54 | 8.29 |

DIAGNOSIS. *Nematopora* with delicate dendroid zoarium. Branches dichotomise irregularly, are straight in outline and subcircular in cross-section. Autozooecia are developed in four to five longitudinal rows on one surface only. Autozooecial apertures are oval and surrounded by small acanthostyles. Reverse surface barren, with four to five longitudinal rows of faint pustules.

DESCRIPTION. Colonies are small, delicate, erect with irregularly dichotomising branches. The largest fragment examined measures 16.4mm in length. Branches are straight (range of diameter from 0.41mm to 0.76mm), sub-circular in cross-section. Branch width increases slightly prior to bifurcation. Interapertural areas may bear one to two rows of small acanthostyles which surround autozooecial apertures. The reverse surface is barren, either smooth or with small acanthostyles occurring in four longitudinal rows (Fig. 7).

Autozooecia are arranged quincuncially in four to five longitudinal rows, irregularly spaced within and between rows.

Autozooecial apertures are oval to ellipical in shape, often narrower distally. Vestibules are steep-sided and shallow distally.

DISCUSSION. From the study area only 22 fragments of *Nematopora hibernica* were found. All are hollow silicified fragments in which only the surface has been replaced, and consequently details of internal morphology are unknown.

Externally *Nematopora* is very distinctive. The rhombic shape of the autozooecial apertures, and the abundance of acanthostyles resembles that of *Rhabdomeson rhombiferum* (Phillips), but unlike the latter autozooecial apertures do not occur all the way around the branch.

*N. hibernica* is only the second species of *Nematopora* to be described from the British Isles *Nematopora hexagona* having been described from the Silurian (Wenlock) of Shropshire (Owen, 1962). Only 27 species of *Nematopora* have been described worldwide throughout its stratigraphic range (Goryunova 1985). Of these only seven, found in the U.S.S.R., Afganistan, and Japan, occur in the Carboniferous: *N. afgana* Termier & Termier, 1971; *N. donbassica*, Dunaeva, 1961; *N. kusbasensis* Trizna, 1958; *N. ivanovi* Shulga-Nesterenko, 1955; *N. parvula* Shulga-Nesterenko, 1955; *N. tulensis* Morozova, 1955; and *N.* sp. indet. Sakagami, 1962.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian).

DISTRIBUTION. Carrick Lough, County Fermanagh, Ireland.

## Genus ***PSEUDONEMATOPORA*** Balakin, 1974

TYPE SPECIES. *Nematopora? turkestanica* Nikiforova, 1948 by original designation from the Lower Carboniferous of the CIS (former Soviet Union).

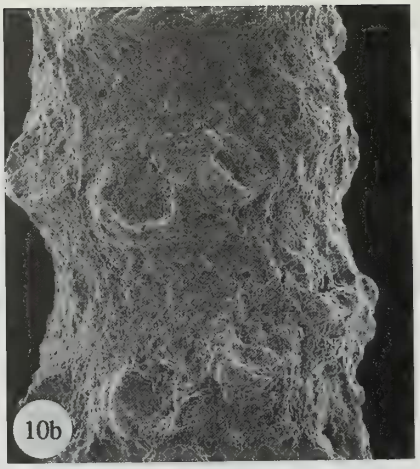
EMENDED DIAGNOSIS. Arthrostylid with slender dendroid zoarium, with occasional dichotomising branches. Branches are of constant width and are circular to semicircular in cross-section. Autozooecia occur in 6 to 16 longitudinal rows, and are budded in an annular manner. Autozooecial apertures are circular to oval in shape, with proximal peristomes. Autozooecia originate from a central axis. Skeletal cysts may be present in the exozone. Terminal diaphragms developed in some species. Acanthostyles are absent.

STRATIGRAPHICAL RANGE. Lower Carboniferous (lower Tournaisian–lower Viséan).

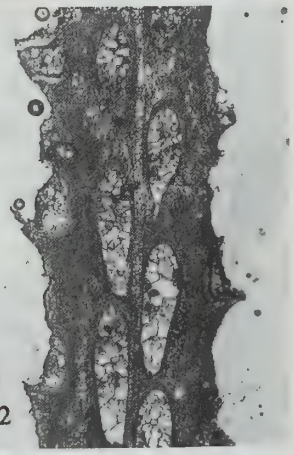
**Table 4** Quantitative comparison between Carboniferous species of *Nematopora* (in mm).

| | AR | BW | AD1 | AD2 | AS1 | AS2 |
|---|---|---|---|---|---|---|
| *N. hibernica* sp. nov. | 5 | 0.41–0.76 | 0.21–0.44 | 0.08–0.20 | 0.11–0.52 | 0.08–0.21 |
| *N. afgana* Termier & Termier, 1971 | – | 0.6-1.5 | – | – | – | – |
| *N. donbassica* Dunaeva, 1961 | – | 0.89–1.20 | 0.24–0.32 | 0.12–0.14 | 0.29–0.36 | 0.12 |
| *N. kusbasensis* Trizna, 1958 | 10 | 0.96–1.00 | 0.18–0.22 | 0.08–0.12 | – | – |
| *N. ivanovi* Shulga-Nesterenko, 1955 | – | 0.70–0.90 | 0.40–0.45 | 0.15 | – | – |
| *N. parvula* Shulga-Nesterenko, 1955 | – | 0.25–0.30 | 0.30–0.35 | 0.07–0.10 | – | – |
| *N. tulensis* Morozova, 1955 | – | 0.30–0.40 | 0.20–0.22 | 0.10 | – | – |
| *N.* sp. indet. Sakagami, 1962 | 8–10 | 1.00–1.10 | 0.24 | 0.13–0.16 | – | – |

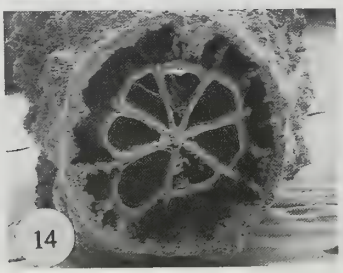
Data from original sources.








DISTRIBUTION. Ireland, England, Belgium, and the CIS (former Soviet Union).

***Pseudonematopora planatus*** sp. nov. Figs 3c, 10–15

HOLOTYPE. BMNH PD9450; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

PARATYPES. BMNH PD9451-9472, 9741; TCD.34018-34025, 34137, 34160, 34161, 42561, 42607; BELUM K2222; all from same locality and horizon as above. TCD.42516-42519, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh

DERIVATION OF TRIVIAL NAME. From the Latin *planus* meaning plain and unornamented.

DIAGNOSIS. *Pseudonematopora* with slender dendroid zoaria. Branches dichotomise infrequently and at a high angle. They are circular to sub-circular in cross-section and are a constant width throughout their length. Autozooecial apertures occur in 6 to 8 longitudinal rows. They are circular in shape and have an arcuate, proximally located, peristomial rim. A faint longitudinal ridge occurs in the smooth interapertural area. Autozooecial budding is annular from a central axis. Chambers diverge at a low angle in the endozone before bending in the exozone to become orientated at an angle of 60° to 70° to the zoarial surface. Zooecial walls are thin in the endozone and do not thicken in the exozone. Terminal diaphragms may be developed. Skeletal cysts are lacking.

DESCRIPTION. Colonies are small, delicate and have irregularly dichotomising straight branches, which are circular in cross-section and undulatory in outline. The largest fragment examined is 13.2 mm in length. On no specimen were two dichotomies seen.

Autozooecia occur in 6 to 8 longitudinal rows around the circumference of the zoarium except for a thin barren area on the reverse. They are budded from a distinct central axis in an annular pattern. Zooecial chambers diverge from the median wall at an angle of 10° to 15° in the endozone. The exozone is reached when the chambers bend fairly abruptly through 60° to 70°. The living chambers are orientated nearly perpendicular to the zoarial surface. The complete chamber is nearly four times as long as it is wide. Interzooecial walls are very thin in the endozone but thicken considerably in the exozone. Basal diaphragms are not developed and the zooecial chambers are simple tubular structures.

Interapertural areas are smooth with a single faint longitudina

**Figs 10–14** *Pseudonematopora planatus* sp. nov. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **10**, BMNH PD9450 (**holotype**); **10a**, colony fragment showing cylindrical branch shape, with circular autozooecial apertures developed in irregular longitudinal rows; apertures surrounded by proximal peristomes that extend beyond the branch margin giving an uneven outline, ×12; **10b**, detail of 10a showing the smooth interapertural areas, ×80. **11**, BMNH PD9452 (paratype), reverse surface showing longitudinal sinuous series of small nodes, ×12. **12**, BMNH PD9470 (paratype), tangential section showing the central axial region with a row of autozooecial either side of it, and the marginal protrusion of the proximal peristmes, ×35. **13**, BMNH PD9471 (paratype); **13a**, longitudinal section showing thin axial region from which are budded autozooecial chambers and the thickened exozone, ×20; **13b**, detail of 13a showing brown bodies in autozooecial chambers trapped behind a thin linear terminal diaphragm (arrowed), ×35. **14**, BMNH PD9452 (paratype), transverse section showing radial arrangement of seven autozooecial chambers around the central axis, ×35.

**Fig. 15** *Pseudonematopora planatus* sp. nov. Line drawing of external features of BMNH PD9450; scale bar = 1 mm.

ridge developed between adjacent autozooecial rows. On the reverse surface the interapertural areas are slightly wider than those on the obverse surface. A strong ridge may be developed there.

Autozooecial apertures are small and circular. The apertures of the autozooecia adjacent to the reverse surface are divergent from it (Fig. 11) and are marginally larger than those in other rows on the obverse surface. Peristomes, situated proximally, are commonly developed around apertures. Thin terminal diaphragms close off some autozooecial apertures, behind which small circular brown bodies are found in chambers (Fig. 13b). These brown bodies, which are similar in morphology to those reported by Morrison & Anstey (1979) in some Ordovician trepostomes, represent the degenerated remains of the polypide soft tissues.

**Table 5** Measurements of *Pseudonematopora planatus* (in mm). N=13.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW | 130 | 0.80 | 0.61 | 1.20 | 7.80 | 7.96 |
| AD1 | 130 | 0.18 | 0.10 | 0.26 | 10.84 | 8.60 |
| AD2 | 130 | 0.13 | 0.10 | 0.23 | 14.74 | 6.08 |
| AS1 | 130 | 0.39 | 0.24 | 0.63 | 15.32 | 6.69 |
| AS2 | 130 | 0.18 | 0.10 | 0.41 | 26.97 | 5.65 |
| Z2 | 130 | 3.6 | 3 | 5 | 11.31 | 13.50 |
| AR | 13 | 7.5 | 6 | 8 | – | 12.89 |

DISCUSSION. *Pseudonematopora* is reported from outside the CIS (former Soviet Union) for the first time. In the County Fermanagh fauna *P. planatus* is quite common. Only three other species have previously been recorded, all from Lower Carboniferous strata: *P. petchorensis* Gorjunova, 1985, the type species *P. turkestanica* (Nikiforova, 1948) [Balakin, 1974], and *P. balakini* Gorjunova, 1988. *P. planatus* differs from these three species in a number of respects. Zoarial width is narrower in *P. turkestanica* and the number of autozooecial rows is less. More importantly the autozooecial apertures in *P. planatus* are at least half the size as those of the other three species. Skeletal cysts are absent in *P. planatus* but may be developed in the other species. Terminal diaphragms have been reported from both *P. turkestanica* (Owen, 1966) and *P. balakini* (Gorjunova, 1988), and are present in *P. planatus*.

Balakin (1974) noted that variation in zoarial width and fluctuation in the number of autozooecial rows in *P. turkestanica* are both large. *P. planatus* does not show such variation. Coefficients of variation for all measured parameters are low (Table 5). Variation within colonies is greater than variation between colonies in all features except zoarial width (ZW) and the number of autozooecia in a 2mm line (Z2). In these two cases variation within and between colonies is virtually identical.

*Rhombopora radialis* Owen, 1966 is herein considered to be conspecific with *Pseudonematopora turkestanica* (Nikiforova, 1948). Comparison of Owen's type material (LL.2984 holotype; LL.2985-2989 paratypes; Upper Viséan; Treak Cliff, Castleton, Derbyshire) with illustrations of *Pseudonematopora turkestanica* from the former Soviet Union (Balakin 1974) shows these taxa to have a similar morphology. *Pseudonematopora* is characterised by autozooecia budded from a central axis in an annular fashion, with short chambers and terminal diaphragms often developed, circular apertures with proximal peristomes, and a lack of acanthostyles and metapores. Conversely, *Rhombopora* zoaria are dendroid, with long autozooecia containing hemisepta, and with oval zooecial apertures, many acanthostyles, and occasionally metapores.

*Pseudonematopora* is a very distinct genus with a straight, occasionally branching zoarium, autozooecia budded from a central axis, apertures with proximal peristomes, and occasional terminal diaphragms. Externally the taxon resembles the cystoporate *Cheilotrypa* Ulrich 1884. However, internal structures and budding patterns in the two are quite different: in *Cheilotrypa* diaphragms are present and autozooecia are budded from a central hollow axial tube (Utgaard 1983).

*Nematopora* has been regarded as ancestral to *Pseudonematopora* (Balakin 1974) because the two taxa display a similar colony shape, autozooecial chamber shape, aperture size and shape, and budding pattern. However, in a computer-based phenetic study on the Rhabdomesina using cluster analysis of 44 features, Blake & Snyder (1987) suggested that *Pseudonematopora* was more closely related to *Osburnostylus* (88% similarity) than to *Nematopora* (78% similarity). Externally, however, *Osburnostylus* with rapid thickening of the zoarium at the level of the autozooecia apertures appears more different from *Pseudonematopora* than is *Nematopora*. Resolution of this phylogenetic problem may be achieved through finds of *Pseudonematopora*, extending its range, both geological and geographical, and by more work on Palaeozoic bryozoans.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Viséan, Asbian).

DISTRIBUTION. Carrick Lough and Sillees River, County Fermanagh, Ireland.

**Table 6** Quantitative comparison between *Pseudonematopora* species (dimensions in mm).

| | BW | AR | AD1 | AD2 | AS1 | AS2 | Z2 |
|---|---|---|---|---|---|---|---|
| *planatus* sp. nov. | 0.61–1.20 | 6–8 | 0.10–0.26 | 0.10–0.23 | 0.24–0.63 | 0.10–0.41 | 3–5 |
| *balakini* Gorjunova, 1988 | 0.88–1.10 | – | 0.35–0.45 | 0.22–0.26 | – | – | 4 |
| *petchorensis* | 0.72–1.08 | – | 0.33–0.36 | 0.15–0.19 | 0.33–0.36 | 0.20–0.25 | 3.5 |
| *turkestanica* (Nikiforova, 1948) | 0.80–2.80 | 8–16 | 0.25–0.37 | 0.17–0.22 | 0.25–0.37 | 0.15–0.25 | 3–4 |

data from original sources.

Family **RHABDOMESIDAE** Vine, 1884a
Genus ***RHABDOMESON*** Young & Young, 1874

TYPE SPECIES. *Millepora gracilis* Phillips, 1841, by monotypy, from the Devonian of north Devon, England (for discussion relating to the problems with this type species see Wyse Jackson & Bancroft 1995a, 1995b).

***Rhabdomeson progracile*** Wyse Jackson & Bancroft, 1995 Fig. 16

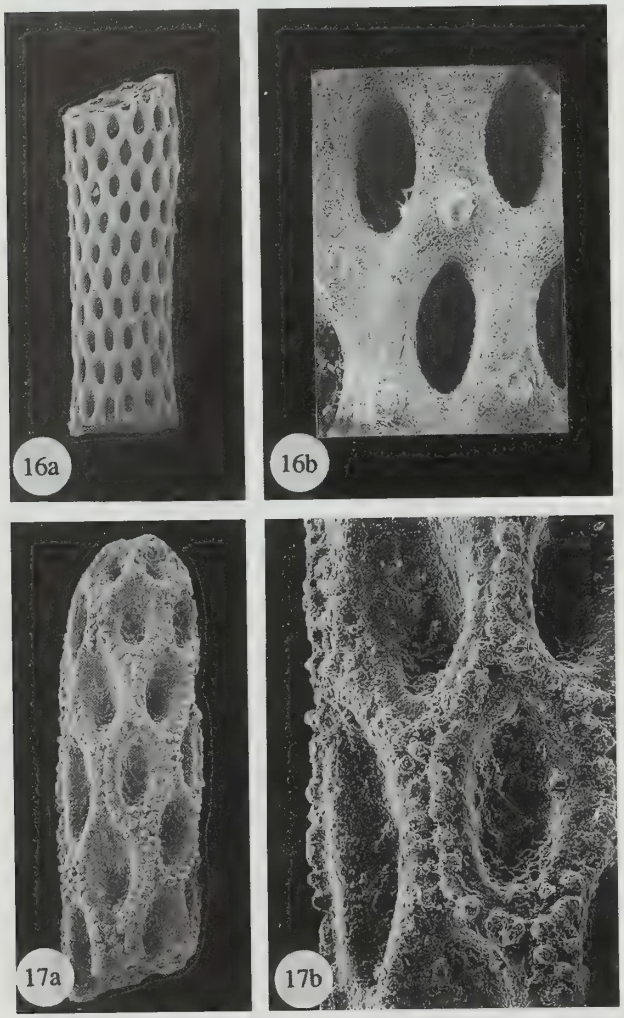



**Fig. 16** *Rhabdomeson progracile* Wyse Jackson & Bancroft 1995. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; BMNH PD9473 (paratype); **16a**, typical zoarial fragment showing cylindrical shape of branch, with the spiral arrangement of autozooecia in curved interlocking rows; autozooecial apertures are oval to elliptical in shape; one large acanthostyle is placed distally of apertures, ×25; **16b**, detail of 16a, ×130.

**Fig. 17** *Rhabdomeson rhombiferum* (Phillips, 1836). Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; BMNH PD9485; **17a**, growing tip of branch showing cylindrical colony form; autozooecia are arranged in longitudinal and obliquely intersecting rows; apertures are oval in shape, and narrow slightly distally; short blunt stylets surround each autozooecial aperture, ×50; **17b**, detail of 17a showing autozooecial aperture surrounded by stylets, ×130.

MATERIAL. BMNH PD9473-9484, TCD.34026-34028, BELUM K3095, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh, Ireland. TCD.42520, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria are dendroid, with cylindrical branches ranging in diameter from 0.61 to 1.07mm. There may be some increase in branch diameter prior to, or subsequent to, lateral branch development. Bifurcation is rare. The longest zoarial fragment examined measures 8.1mm in length.

Autozooecia are budded from a straight hollow cylindrical axis 0.14 to 0.29mm in diameter, in an annular or spiral pattern. In thin section autozooecial chambers are triangular to pentagonal in shape when seen in transverse section. Vestibules are orientated at a high angle to the zoarial surface. Acanthostyles arise as rods of granular calcite in the lower portions of the exozone. Interchamber endozonal walls are 0.1mm in width and are composed of an inner granular layer surrounded by a fine laminated skeleton.

Autozooecial apertures are pyriform to oval in shape, and moderate to small in size. They are crowded or arranged in quincunx in 14 to 18 longitudinal rows around the branch. Interapertural spacing is greatest longitudinally where apertures are spaced one diameter apart and up to 5 in a 2mm line. Transversely adjacent apertures are spaced less than one diameter apart. Autozooecial apertural dimensions and spacing are approximately constant in each branch fragment. However, some considerable differences are found between zoarial fragments.

A large acanthostyle, up to 0.12mm in height, is always found distal to autozooecial apertures. Rare zoaria bear only this single acanthostyle (Fig. 16b); more frequently one or two smaller acanthostyles lie proximal to the first in a longitudinal line between adjacent autozooecial apertures. Acanthostyles are usually abraded, and appear as faint protruberances on the zoarial surface.

DISCUSSION. A complete systematic description of *R. progracile* is given in Wyse Jackson & Bancroft (1995a).

***Rhabdomeson rhombiferum*** (Phillips, 1836) Fig. 17

MATERIAL. BMNH PD9485-9506; TCD.34029-34036, 42591b, 42593a, 42595; BELUM K3045, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. Ireland; TCD.42521-42524, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. The dendroid zoarium is composed of irregularly bifurcating delicate branches, with a polygonal or circular cross-section, that range in diameter from 0.41 to 0.86mm. Branch width remains approximately constant along their entire lengths. Branching either by bifurcation or development of lateral branches at a high angle of between 68° and 90° from parent branch. There is no increase in branch diameter prior to or subsequent to branch development. In no specimen was there more than one bifurcation or lateral branch observed.

Autozooecial apertures are moderate to large in size, pyriform to oval or ellipsoidal in shape, and are arranged in quincunx in eight to eleven longitudinal rows around branches.

Apertural size, shape and spacing is very variable around the branch. A distinct barren area 0.25mm in width, with four longitudinal rows of small acanthostyles, is found on some branches and can be regarded as delineating the branch reverse surface. In all zoaria the autozooecial apertures are long, thin, and oval in shape on the reverse surface. Towards the obverse surface apertures become

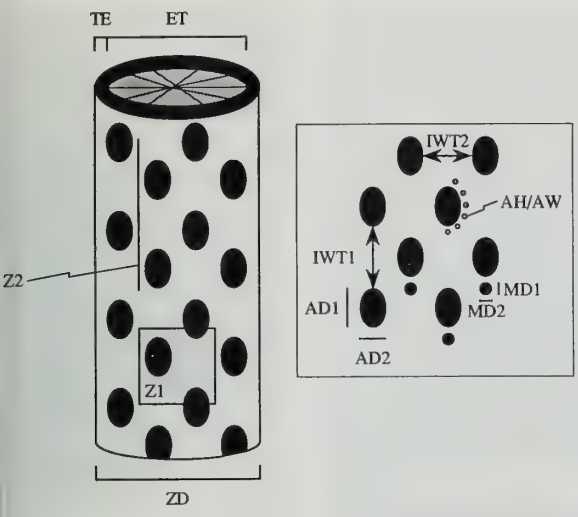



**Fig. 18** Measurements taken on rhomboporid and hyphasmoporid cryptostomes in this study: ZD = Width of zoarium measured perpendicular to growth direction; MD = Metapore diameter; MD1 = Metapore diameter measured parallel to growth direction; MD2 = Metapore diameter measured perpendicular to growth direction; AH = Acanthostyle height from base to tip; AW = Acanthostyle width measured at its base; AD1 = Autozooecia apertural diameter measured parallel to growth direction; AD2 = Autozooecia apertural diameter measured perpendicular to growth direction; IWT1 = Autozooecia apertural spacing measured parallel to growth direction; IWT2 = Autozooecia apertural spacing measured perpendicular to growth direction. Z1 = Number of autozooecial apertures contained in $1mm^2$; Z2 = Number of autozooecial apertures contained within a 2mm line measured parallel to growth direction; AR = Number of autozooecial apertural rows measured around zoarium; ET = Endozone thickness; TE = Exozone thickness.

ncreasingly pyriform and equidimensional. This variation in pertural size is reflected in apertural spacing; these two parameters apertural size and apertural spacing) are inversely proportional to ach other. Immediately after branching, elongate autozooecial pertures developed around the complete circumference of the aughter branch. Differentiation of apertural dimensions occurs istally within two or three generations along the branch.

Interapertural walls are gently sinuous or occasionally straight nd may be raised to produce a ridge between apertural rows. One or wo rows of small short acanthostyles (0.02–0.04mm in diameter) re developed along this ridge. When two rows are present they are eparated by a distinct furrow.

Autozooecial apertures are surrounded by 24 to 30 acanthostyles, n various patterns. Commonly they flank only lateral margins and p to six acanthostyles may occur proximal to apertures. Less equently acanthostyles are arranged in a rhombic pattern, with nly one acanthostyle proximal to apertures.

DISCUSSION. A complete systematic description of *Rhabdomeson hombiferum* is given in Wyse Jackson & Bancroft (1995a), as well s a discussion of budding, branching and other features in habdomesonids.

## Family **RHOMBOPORIDAE** Simpson, 1895
## Genus ***RHOMBOPORA*** Meek, 1872

YPE SPECIES. *Rhombopora lepidodendroides* Meek, 1872 by original designation, from the Upper Carboniferous of Nebraska City, Nebraska, U.S.A.

### ***Rhombopora cylindrica*** sp. nov. Figs 19–25

| | |
|---|---|
| *non* 1841 | *Millepora similis* Phillips: 21, fig.32. |
| *non* 1843 | *Millepora similis* Phillips; Morris: 42. |
| 1844 | *Millepora similis* Phillips; M'Coy: 196. |
| *non* 1854 | *Ceriopora similis* (Phillips); Morris: 121. |
| 1854b | *Millepora similis* Phillips; M'Coy: 104. |
| 1862 | *Millepora similis* Phillips; Griffith: 196. |
| 1871 | *Ceriopora similis* (Phillips); Young & Armstrong: 33. |
| 1876 | *Ceriopora similis* (Phillips); Armstrong, Young & Robertson: 46. |
| 1877 | *Ceriopora similis* (Phillips); Young & Robertson: 175. |
| 1881 | *Ceriopora similis* (Phillips); Vine: 338. |
| 1885 | *Rhombopora similis*? (Phillips); Vine: 93 *pro parte*. |
| *non* 1887 | *Rhombopora persimilis* Ulrich; Vine: 226, pl.1, fig.6. |
| 1887 | *Rhombopora similis* (Phillips); Vine: 226, pl.1, fig.7. |
| 1889 | *Rhombopora similis* (Phillips); Vine: 198. |
| 1987 | *Rhombopora similis* (Phillips); Bancroft: 196. |

HOLOTYPE. BMNH PD9507; Upper part of the Glencar Limestone, Lower Carboniferous (Viséan, Asbian); Carrick Lough, County Fermanagh.

PARATYPES. BMNH PD9508-9534, 9576, upper part of the Glencar Limestone, Lower Carboniferous (Viséan, Asbian); Carrick Lough, County Fermanagh; Tavener-Smith and Wyse Jackson Collections. BMNH D294 (2 zoaria in a cavity slide of five), D295, Lower Carboniferous, Gayton Boring, Northamptonshire, England; Vine Collection. BMNH D303 (thin section of several zoarial fragments), Shales; Lower Carboniferous; Argyleshire, Scotland; Vine Collection. TCD.28317, 28369, Nant-y-Gamar buildup, Llandudno Pier Dolomite Formation (Viséan, Asbian), near Llandudno, north Wales. TCD.34037-34044, 34122, 34126, 34128, 34165, 42592a, b; BELUM K2175, Upper part of the Glencar Limestone, Lower Carboniferous (Viséan, Asbian); Carrick Lough, County Fermanagh; Wyse Jackson Collection. TCD.41515, Shales above Main Limestone, Pendleian, Upper Carboniferous, Hurst, near Richmond, Yorkshire, U.K. [NZ044 023], Bancroft Collection. TCD.42525-42528, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh, Wyse Jackson Collection.

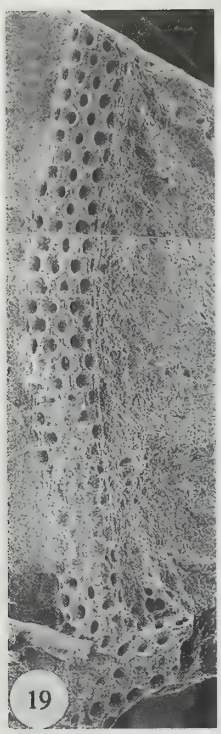
DERIVATION OF NAME. From the cylindrical nature of zoarial branches.

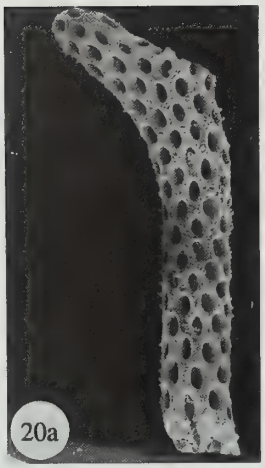
DIAGNOSIS. *Rhombopora* with zoaria comprised of irregularly dividing, thin, cylindrical branches. Autozooecia are budded in a spiral manner from a central linear axis. The exozone region is thin. Autozooecial apertures are oval in shape, moderate to large in size and arranged in quincunx in longitudinal rows around branches. Metapores are rare and occur proximal to autozooecial apertures. Stylets are common and structurally varied: characteristically one to two acanthostyles may be situated at junctions of interapertural walls, and many small heterostyles occur in interapertural areas.

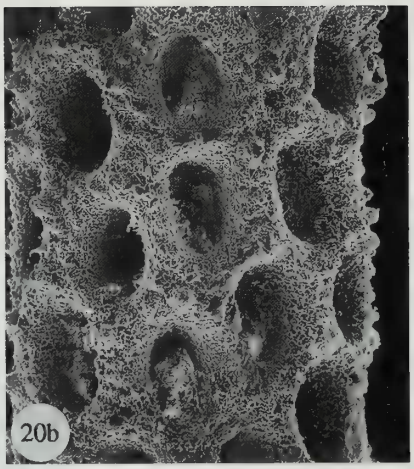
DESCRIPTION. Colonies are composed of delicate, thin bifurcating branches. The largest fragment examined measures 16.2mm in length.

Branches range in diameter from 0.54 to 1.15mm and retain a constant width along their length except prior to lateral branch development when a 25% increase in diameter occurs. Bifurcation is infrequent and irregular; lateral ramifications deviate at high angles of between 75° and 87°.

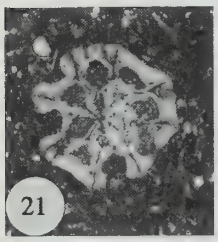
Autozooecia are budded from a straight to undulatory central axis

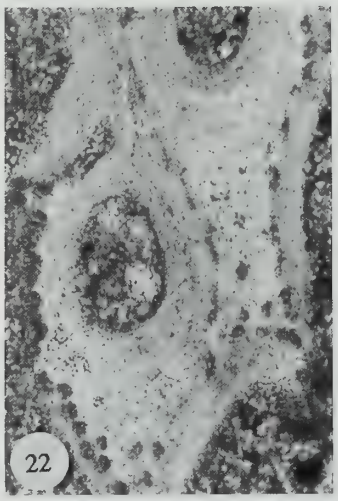


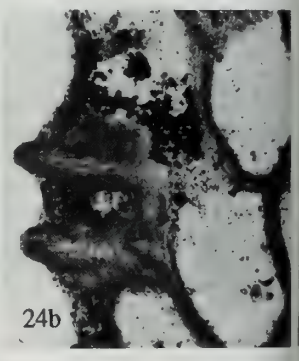












**Figs 19–24** *Rhombopora cylindrica* sp. nov.; **19–23**, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **19**, BMNH PD9509 (paratype), colony form showing long straight branches, with interconnected longitudinal and oblique rows of autozooecia, ×20; **20**, BMNH PD9507 **(holotype)**; **20a**, zoarial fragment with distal growing tip, showing regular arrangement of autozooecial apertures around branch; large acanthostyles are situated at the proximal and distal ends of apertures with smaller heterostyles developed on surrounding walls, ×20; **20b**, detail of 20a showing autozooecial apertures and acanthostyles on interapertural walls, ×110; **21**, BMNH PD9534 (paratype), transverse section showing radial budding pattern of autozooecia and the differentiation of endozone and exozone; **22**, BMNH PD9532 (paratype), tangential section showing oval-shaped autozooecia and heterostyles (C-type stylets) developed on interapertural walls, ×100; **23**, BMNH PD9531, (paratype), longitudinal section showing autozooecial chamber shape and the thickened exozonal walls, ×40; **24**; Shales above Main Limestone, Pendleian, Upper Carboniferous, Hurst, near Richmond, Yorkshire, U.K. TCD.41515; **24a**, longitudinal section, ×25; **24b**, detail of 24a showing morphology of acanthostyles, ×80.

at low angles of 10° to 25° and chambers are eight times as long as their maximum width. The chamber bends through 30° to 40° at the endozone/exozone boundary and vestibules are orientated at an angle of 45° to the zoarial surface. In cross-section chambers are rhombic, pentagonal or subcircular in shape. Chamber walls are thin (0.01–0.03 mm), compound (a very thin granular core covered by laminated skeleton) in the endozone and thicker, with a predominantly laminated skeleton, in the narrow exozone region. The exozone varies in width between 0.1 and 0.2 mm and is approximately one fifth the width of branches. Thin terminal diaphragms may be present.

Autozooecial apertures are large to moderate in size, oval to circular in shape, regularly spaced approximately one diameter apart, and spirally arranged in quincunx in 10 to 16 longitudinal rows around branches. 3 to 6 apertures occur longitudinally and 8 to 10 diagonally along a 2mm line. Autozooecial apertural size is constant on a zoarium except at branch nodes. The first autozooecial apertures on new branches are long and thin, particularly on the reverse surface of branches. Uniformity of size is regained 4 to 5 apertures along branches. Metapores are rare. They are small (0.01–0.13 × 0.02–0.10mm), irregular in shape and one or occasionally two are found proximal of autozooecial apertures, with others sparsely distributed elsewhere on interapertural walls. They are usually developed close to branch divisions and zoarial thickenings. They originate within the exozone.

Stylets are numerous and structurally varied. They occur in one or two rows, between autozooecial apertures. One or rarely two acanthostyles (up to 0.07mm wide) occur at autozooecial apices or


**Fig. 25** *Rhombopora cylindrica*: sp. nov. Line drawing of external features of BMNH PD9507; scale bar = 1 mm.

some but not all zoaria. 20 to 24 heterostyles (0.01–0.03mm wide) in one or two rows flank autozooecial apertures on all zoaria. A longitudinal groove frequently occurs between heterostyle rows which probably marks the position of the zooecial boundary. Acanthostyles have a thick granular core and develop from the base of the exozone. Heterostyles have a thinner granular core and grow from within the exozone. Skeletal lamellae are bent around acanthostyles.

**Table 7** Measurements of *Rhombopora cylindrica* (in mm). N=23.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 187 | 0.76 | 0.54 | 1.15 | 4.40 | 7.11 |
| Z1 | 4 | 8.75 | 8 | 10 | 10.94 | – |
| Z2 | 155 | 4.26 | 3 | 6 | 9.56 | 10.57 |
| AD1 | 219 | 0.19 | 0.10 | 0.35 | 12.22 | 7.21 |
| AD2 | 219 | 0.11 | 0.07 | 0.18 | 12.18 | 8.56 |
| WT1 | 219 | 0.25 | 0.12 | 0.55 | 18.87 | 6.80 |
| WT2 | 219 | 0.15 | 0.09 | 0.32 | 24.78 | 6.55 |
| MD1 | 21 | 0.04 | 0.01 | 0.13 | 32.17 | 2.04 |
| MD2 | 21 | 0.04 | 0.02 | 0.10 | 24.85 | 2.10 |
| AH | 34 | 0.04 | 0.01 | 0.10 | 27.86 | 1.79 |
| AW | 63 | 0.02 | 0.01 | 0.07 | 20.64 | 2.01 |
| TE | 18 | 0.15 | 0.10 | 0.20 | 13.53 | 5.66 |

DISCUSSION. *Rhombopora cylindrica* is quite distinctive and may be easily distinguished by the presence of oval-circular autozooecial apertures, a central axis, a thin exozone, and structurally varied acanthostyles.

Coefficients of variation for both zoarial (ZW) and zooecial (AD1, AD2, IWT1, and IWT2) parameters within colonies are low. CVw values for metapore diameter (MD1 and MD2) as well as acanthostyle height (AH) and width (AW) are large. They are due to the space-filling function of metapores, abrasion of acanthostyles, and poor replacement by silica of small skeletal elements. This is reflected by examining autozooecia aperture dimensions which were more varied in silicified specimens than in calcified specimens. Coefficients of variation between colonies are all extremely low.

*Millepora similis* was first described by Phillips (1841) as a supposed coral from the Devonian of south-west England. Phillips collected specimens from two localities: Cannington Park, north Devon, and Hope, near Torquay, south Devon. M'Coy (1844) noted *Millepora similis* from the Lower Carboniferous of Ireland (the Courceyan of St. Doulagh's, County Dublin and the Courceyan/Chadian of Gort, County Galway). This identification was the first of many that confused two distinct taxa of Devonian and Carboniferous age. It is unfortunate that of the two slabs labelled *Millepora similis* from the Griffith Collection (NMING F7081, 7082) examined by M'Coy neither contains specimens referable to either taxa; but it is evident that M'Coy described a taxon that is different from the Devonian *Millepora similis* of Phillips (M'Coy, 1844: 196).

Subsequently Morris (1854) classified *Millepora* as a zoophyte and transferred *M. similis* into the genus *Ceriopora,* considered then to be a coral, but now known to be a cyclostome bryozoan.

Later still, Young & Robertson (1877) described some Carboniferous bryozoans from the Carboniferous of Scotland, which they regarded as being conspecific with *Ceriopora similis*. Vine (1881) followed this description but later (1885) deciding that the former generic assignment was incorrect, placed all Carboniferous material, as well as Phillips' Devonian taxon, into the newly erected genus *Rhombopora* Meek, 1872.

*Rhombopora similis* (Phillips, 1841) *sensu* Vine 1885 has only been found in strata of Carboniferous age. It is clear that M'Coy (1844) misassigned a new undescribed Lower Carboniferous bryozoan and that this mistake was compounded and reinforced in later descriptions of Lower Carboniferous material.

Phillips' figured and only extant *Millepora similis* specimen (GSM 7110, ?Hope's Nose Limestone, Middle Devonian (Eifelian), Hope, near Torquay, Devon, England) has been examined. It is a poorly preserved specimen which displays both rhomboporid and ptilodictyid affinities. The zoarium is composed of dendroid, moderately delicate, flattened lense-shaped straight bifurcating branches 1.35–1.80mm in diameter. Autozooecia are developed in eight to ten longitudinal rows. Autozooecial apertures are moderately large, 0.28 × 0.13mm, distinctly rhombic in shape, and closely packed less than one diameter apart. Interapertural walls are thin and appear to be smooth. A single proximal acanthostyle may be associated with autozooecial apertures. These features contrast with the cylindrical branches and oval to circular-shaped autozooecial apertures developed in *R. cylindrica.*

Vine's figured material (BMNH D294-5: Vine 1887, pl.1, figs 7–8) in the collections of the Natural History Museum, London, and some Vine material in National Museum of Wales, Cardiff has been examined, and all specimens are correctly assigned to the genus *Rhombopora*. They are not conspecific with Phillips' Devonian taxon.

The Carboniferous material represents a new taxon which is described and named here as *Rhombopora cylindrica*. A new epithet is required; *similis* of M'Coy cannot be used on account of original misapplication of the name through misidentification (Article 49 – *Code of Zoological Nomenclature,* 1985).

A holotype for *Rhombopora cylindrica* sp. nov. is designated from the Lower Carboniferous of Carrick Lough, County Fermanagh, Ireland.

STRATIGRAPHICAL RANGE. Carboniferous (Asbian–Pendleian). The range of *Rhombopora cylindrica* has been increased downwards into the Asbian by its discovery in County Fermanagh and Nant-y-Gamar, north Wales, where the taxon is quite uncommon.

DISTRIBUTION. Carrick Lough and Sillees River, County Fermanagh and Nant-y-Gamar, north Wales. Previously recorded and described (see discussion) from the Brigantian of the Midland Valley of Scotland (Young & Armstrong 1871, Young & Robertson 1877)

and the Arnsbergian of Northamptonshire (Vine 1887) and Lancashire (Vine 1885), and the Pendleian of Yorkshire (Bancroft 1984, Vine 1881).

***Rhombopora hexagona*** sp. nov. Figs 26–31

HOLOTYPE. BMNH PD9535, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

PARATYPES. BMNH PD9536-9564; TCD.34045-34048, 34121, 34154, 34170, 42591a, 42592c, 42602a; BELUM K2186, from the same locality and horizon as above; TCD.25687, near base of *Michelinia* Beds, Hook Head Formation (Courceyan), Locality 8 (of Dresser 1960), Lyraun Cove, Hook Head, County Wexford; TCD.25884, *Michelinia* Beds, Hook Head Formation (Courceyan), Locality 15 (of Dresser 1960), Brecaun Church, Hook Head, County Wexford; TCD.25885, *Michelinia* Beds, Hook Head Formation (Courceyan), Locality 40 (of Dresser 1960), Patrick's Bay, Hook Head, County Wexford; TCD.25886, *Linoproductus* Beds, Hook Head Formation (Courceyan), Locality 92 (of Dresser 1960), Hook Head, County Wexford.

DERIVATION OF TRIVIAL NAME. From the hexagonal pattern of heterostyles disposed around autozooecial apertures.

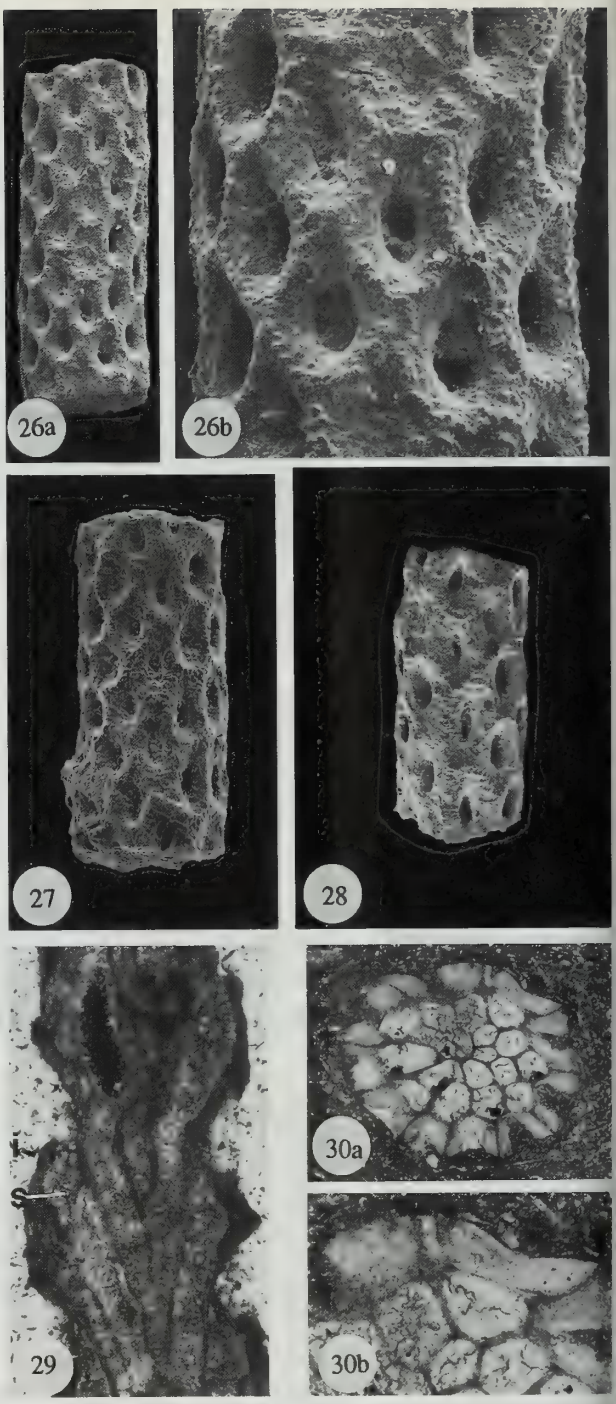
DIAGNOSIS. *Rhombopora* with thin dichotomising cylindrical branches. Autozooecia are budded from a central linear axis in a spiral manner. Hemisepta are common: a robust inferior hemiseptum is present at the base of the vestibule while a thin superior hemiseptum is found on distal chamber walls high in the endozone. Diaphragms are absent. Autozooecial apertures are oval in shape, vary in size around branches, and are arranged in intersecting oblique and longitudinal rows around the zoarium. Small heterostyles are arranged on ridges between autozooecial chambers in an interlocking hexagonal pattern.

DESCRIPTION. Zoaria are composed of thin cylindrical dichotomising branches that form delicate erect dendroid colonies. No complete colonies were observed: the largest fragment measured 3.38mm in length.

Branching is infrequent and irregular with either dichotomous bifurcation or lateral perpendicular ramification, producing secondary branches which are slightly narrower than those from which they were derived. All branches retain a constant width along their length.

Autozooecia deviate from a central axis in a spiral fashion at low angles of 18° to 27°. Chambers are sub-linear in shape, five to six times long as wide, with a slightly attenuated zooecial base. Chambers bend marginally at the exozone and vestibules are orientated at low angles of between 25° and 40° to the zoarial surface. Chamber walls are thin (0.01 mm) in the endozone, with a compound structure of a granular centre surrounded by thin skeletal laminae. The exozone is very thin (0.03–0.15mm). In cross-section chambers are polygonal in shape.

Autozooecial apertures are large to moderate in size, oval in shape, and arranged in 9 to 15 longitudinally and diagonally intersecting rows around branches. The angle of this intersection varies from 45° to 75°. Long, narrow autozooecial apertures occur on reverse surfaces, while more equidimensional apertures are found towards and on obverse surfaces. Interapertural spacing is inversely proportional to apertural size (see Tables 9 and 12, and Figs 26a and 28). Autozooecial apertures are surrounded by as many as 40 small, blunt, circular heterostyles (0.01mm in diameter) which arise from the base of, or from within the exozone. They are arranged in single, or occasionally several (particularly on reverse surfaces), rows along the crests of otherwise smooth interapertural walls, or occasionally




**Figs 26–30** *Rhombopora hexagona* sp. nov. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **26**, BMNH PD9535 (**holotype**); **26a**, colony form, ×25; **26b**, detail of 26a showing oval autozooecial apertures and disposition of heterostyles in a hexagonal pattern on interapertural walls, ×75; **27**, BMNH PD9536 (paratype), colony fragment, ×40; **28**, BMNH PD9537 (paratype), view of 'reverse' surface showing long, thin autozooecial apertures, ×25; **29**, BMNH PD9560 (paratype), longitudinal section showing autozooecial chambers with thin superior (labelled 's') and thick inferior (labelled 'i') hemisepta, ×35; **30**, BMNH PD9563 (paratype); **30a**, transverse section showing circular branch outline, zooecia budded from a central axial area, with thin walls in the endozone and thicker walls in the exozone, ×35; **30b**, detail of 30a showing heterostyles on interapertural walls, ×75.

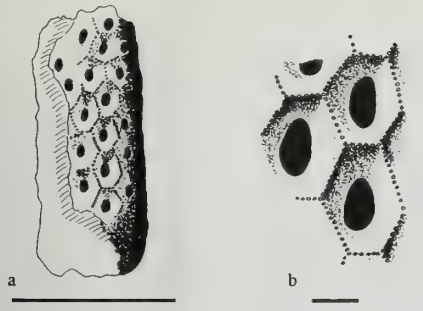
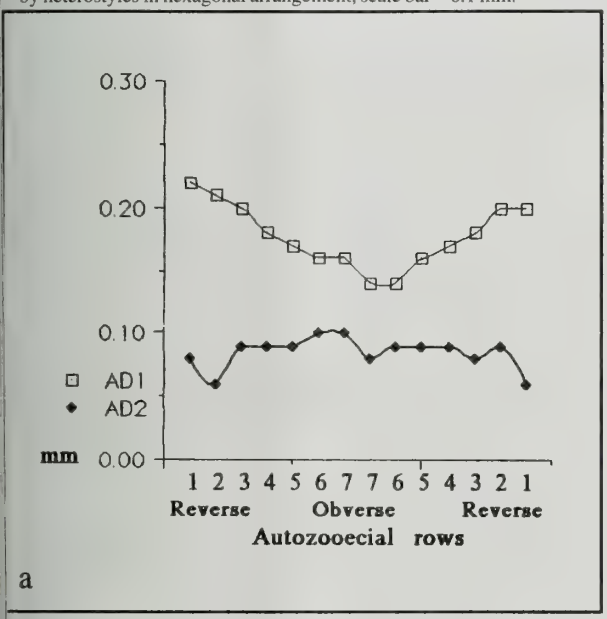
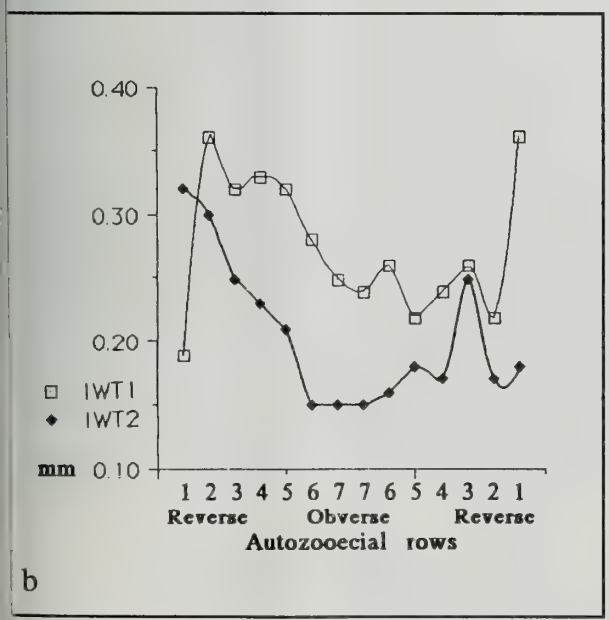



**Fig. 31** *Rhombopora hexagona* sp. nov. Line drawings of external features; **a**, colony form; scale bar = 1 mm; **b**, autozooecial apertures surrounded by heterostyles in hexagonal arrangement, scale bar = 0.1 mm.




**ig. 32** *Rhombopora hexagona* sp. nov. Graphs of mean values of aperture size and spacing; **a**, apertural size; **b**, apertural spacing. (For explanation of AD1, AD2, IWT1 and IWT2 see Fig. 18).

in an interlocking hexagonal to pentagonal pattern. These hexagons range in size from 0.66 × 0.25mm to 0.23 × 0.20mm, with the greatest dimensions occurring on reverse surfaces. Autozooecial apertures are generally situated distally within these areas.

Hemisepta are common and are of two types. A prominent superior hemiseptum occurs within the endozone four-fifths along the chamber on distal walls (Fig. 29). They are thin, short (0.04–0.06mm) and have a similar skeletal structure to chamber walls. At the exozone the proximal chamber walls bend through 30° and thicken rapidly to form robust inferior hemisepta 0.13 long by 0.04mm thick. These have a sharp pointed distal extremity and bend marginally into the vestibules. They are composed of laminated skeleton in which lamellae are orientated parallel to the zoarial surface.

**Table 8** Measurements of *Rhombopora hexagona* (in mm). N=19.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 135 | 0.63 | 0.48 | 0.92 | 4.62 | 7.71 |
| Z2 | 25 | 5.23 | 4 | 6 | 9.93 | 7.75 |
| AD1 | 145 | 0.16 | 0.10 | 0.26 | 20.94 | 8.32 |
| AD2 | 146 | 0.09 | 0.04 | 0.18 | 15.57 | 5.13 |
| IWT1 | 139 | 0.26 | 0.12 | 0.66 | 30.34 | 3.74 |
| IWT2 | 136 | 0.17 | 0.07 | 0.39 | 27.71 | 4.37 |
| AH | 14 | 0.01 | 0.01 | 0.01 | 50.00 | – |
| AW | 31 | 0.01 | 0.01 | 0.02 | 16.04 | – |
| ET | 21 | 0.43 | 0.32 | 0.50 | 5.72 | 8.75 |
| TE | 42 | 0.08 | 0.03 | 0.15 | 17.37 | 2.96 |

DISCUSSION. *Rhombopora hexagona* is only the second species of the taxon, after *R. cylindrica*, to be recorded from Carboniferous strata of the British Isles and has previously been noted from Courceyan strata of Hook Head, County Wexford (Dresser 1960 MS). A previously recorded species *R. radialis* Owen, 1966 from the Viséan of Derbyshire is regarded as being an arthrostylid rather than a rhomboporid and is reassigned to the genus *Pseudonematopora*.

*Rhombopora hexagona* is easily recognised externally from its cylindrical branches on which autozooecial apertures of varying dimensions (which is unusual) are surrounded by a hexagonal pattern of small heterostyles, and internally by the possession of two hemisepta of different sizes and a thin exozone.

The relationship between autozooecial apertural diameter and apertural spacing is illustrated graphically in Fig. 32. Where apertures are long (high AD1) and thin (low AD2) longitudinal autozooecial spacing is moderate (low-high IWT1), and autozooecial spacing between adjacent rows is great (high IWT2). Where apertures are short and fat (low AD1 values; high AD2 values), autozooecial spacing tends to be moderate and narrow (moderate IWT1 values; low IWT2 values). There is an inverse correlation between autozooecial apertural diameters AD1 and AD2 (Fig. 32a) and a moderately positive correlation between autozooecial apertural spacing IWT1 and IWT2 (Fig. 32b). In one specimen (C on Tables 9–12) where 14 autozooecial rows, as against the mean of 10, are developed, these correlations are not good.

Dimensions of 56 other Carboniferous *Rhombopora* taxa are tabulated below. *R. hexagona* differs sufficiently from them, both morphologically and dimensionally, to justify its erection as a new species. It most closely resembles *R. attenuata* Ulrich 1890, in which two acanthostyle types are present, and *R. gracilis* Ulrich 1890, in which acanthostyles are developed at interapertural wall junctions only, but differs in acanthostyle development as well as in the size and spacing of autozooecial apertures.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Courceyan–Asbian).

**Table 9** Measurements of autozooecial aperture length (**AD1**) of *Rhombopora hexagona* around the zoarium from reverse to obverse surface (in mm). N=9 (A–I).

| Reverse | | | | | | Obverse | | | | | | Reverse | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ROW | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| A | – | – | 0.17 | 0.15 | 0.15 | 0.13 | 0.15 | 0.15 | 0.14 | 0.13 | 0.18 | 0.18 | – | – |
| B | – | – | 0.13 | 0.21 | 0.17 | 0.13 | 0.16 | 0.13 | 0.11 | 0.12 | 0.10 | 0.17 | – | – |
| C | 0.22 | 0.18 | 0.19 | 0.18 | 0.16 | 0.13 | 0.13 | 0.12 | 0.12 | 0.13 | 0.13 | 0.17 | 0.20 | 0.20 |
| D | – | – | 0.23 | 0.13 | 0.23 | 0.17 | 0.15 | 0.13 | 0.13 | 0.14 | 0.15 | 0.22 | – | – |
| E | – | – | 0.19 | 0.23 | 0.17 | 0.17 | 0.20 | 0.10 | 0.10 | 0.14 | 0.14 | 0.16 | – | – |
| F | – | – | – | 0.17 | 0.12 | 0.18 | 0.22 | 0.20 | 0.16 | 0.21 | 0.22 | – | – | – |
| G | – | – | – | 0.18 | 0.19 | 0.25 | 0.18 | 0.20 | 0.22 | 0.30 | 0.22 | 0.22 | – | – |
| H | – | – | 0.25 | – | 0.21 | 0.20 | 0.18 | 0.16 | 0.14 | 0.15 | 0.18 | – | – | – |
| I | – | 0.24 | 0.26 | 0.23 | 0.17 | 0.16 | 0.12 | 0.14 | 0.17 | 0.15 | 0.21 | 0.20 | – | – |
| x | 0.22 | 0.21 | 0.20 | 0.18 | 0.17 | 0.16 | 0.16 | 0.14 | 0.14 | 0.16 | 0.17 | 0.18 | 0.20 | 0.20 |

**Table 10** Measurements of autozooecial aperture width (**AD2**) of *Rhombopora hexagona* around the zoarium from reverse to obverse surface (in mm). N=9 (A–I).

| **Reverse** | | | | | | **Obverse** | | | | | | **Reverse** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ROW | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| A | – | – | 0.08 | 0.07 | 0.08 | 0.08 | 0.09 | 0.08 | 0.08 | 0.07 | 0.09 | 0.07 | – | – |
| B | – | – | 0.09 | 0.07 | 0.12 | 0.10 | 0.10 | 0.07 | 0.08 | 0.08 | 0.07 | 0.06 | – | – |
| C | 0.08 | 0.08 | 0.10 | 0.06 | 0.09 | 0.10 | 0.10 | 0.08 | 0.10 | 0.09 | 0.09 | 0.08 | 0.09 | 0.06 |
| D | – | – | 0.12 | 0.08 | 0.09 | 0.12 | 0.18 | 0.08 | 0.08 | 0.09 | 0.08 | 0.12 | – | – |
| E | – | – | 0.09 | 0.08 | 0.07 | 0.07 | 0.06 | 0.07 | 0.08 | 0.06 | 0.07 | 0.07 | – | – |
| F | – | – | – | 0.16 | 0.13 | 0.14 | 0.14 | 0.11 | 0.11 | 0.13 | 0.13 | – | – | – |
| G | – | – | – | 0.11 | 0.11 | 0.10 | 0.11 | 0.10 | 0.09 | 0.12 | 0.15 | 0.13 | – | – |
| H | – | – | – | 0.12 | 0.10 | 0.12 | 0.11 | 0.11 | 0.10 | 0.10 | 0.10 | – | – | – |
| I | – | 0.04 | 0.06 | 0.08 | 0.07 | 0.09 | 0.08 | 0.08 | 0.09 | 0.11 | 0.08 | 0.07 | – | – |
| x | 0.08 | 0.06 | 0.09 | 0.09 | 0.09 | 0.10 | 0.10 | 0.08 | 0.09 | 0.09 | 0.09 | 0.08 | 0.09 | 0.06 |

**Table 11** Measurements of interapertural wall thickness (**IWT1**) of *Rhombopora hexagona* around the zoarium from reverse to obverse surface (in mm). N=9 (A–I).

| **Reverse** | | | | | | **Obverse** | | | | | | **Reverse** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ROW | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| A | – | – | 0.19 | 0.18 | 0.35 | 0.31 | 0.13 | 0.15 | 0.20 | 0.18 | 0.18 | 0.21 | – | – |
| B | – | – | 0.42 | 0.29 | 0.54 | 0.28 | 0.25 | 0.23 | 0.35 | 0.30 | 0.26 | 0.30 | – | – |
| C | 0.19 | 0.22 | 0.20 | 0.17 | 0.24 | 0.25 | 0.28 | 0.26 | 0.30 | 0.22 | 0.20 | 0.20 | 0.22 | 0.36 |
| D | – | – | – | 0.21 | 0.13 | 0.21 | 0.12 | 0.16 | 0.13 | 0.15 | – | – | – | – |
| E | – | – | 0.24 | 0.26 | 0.21 | 0.23 | 0.34 | 0.15 | 0.16 | 0.16 | 0.35 | 0.32 | – | – |
| F | – | – | – | 0.43 | 0.35 | 0.32 | 0.18 | 0.23 | 0.13 | 0.12 | 0.14 | – | – | – |
| G | – | – | 0.64 | 0.48 | 0.30 | 0.37 | 0.34 | 0.37 | 0.39 | 0.24 | 0.28 | – | – | – |
| H | – | – | – | 0.52 | 0.40 | 0.37 | 0.34 | 0.30 | 0.33 | 0.32 | 0.16 | – | – | – |
| I | – | 0.51 | 0.24 | 0.43 | 0.40 | 0.24 | 0.30 | 0.33 | 0.35 | 0.36 | 0.40 | 0.30 | – | – |
| x | 0.19 | 0.36 | 0.32 | 0.33 | 0.32 | 0.28 | 0.25 | 0.24 | 0.26 | 0.22 | 0.24 | 0.26 | 0.22 | 0.36 |

**Table 12** Measurements of interapertural wall thickness (**IWT2**) of *Rhombopora hexagona* around the zoarium from reverse to obverse surface (in mm). N=9 (A–I).

| **Reverse** | | | | | | **Obverse** | | | | | | **Reverse** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ROW | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| A | – | – | 0.24 | 0.23 | 0.18 | 0.17 | 0.16 | 0.21 | 0.22 | 0.22 | 0.13 | 0.26 | – | – |
| B | – | – | 0.17 | 0.31 | 0.39 | 0.17 | 0.20 | 0.21 | 0.17 | 0.23 | 0.22 | 0.29 | – | – |
| C | 0.32 | 0.35 | 0.30 | 0.21 | 0.29 | 0.15 | 0.13 | 0.11 | 0.12 | 0.13 | 0.13 | 0.18 | 0.17 | 0.18 |
| D | – | – | – | 0.17 | 0.10 | 0.21 | 0.22 | 0.20 | 0.23 | 0.19 | – | – | – | – |
| E | – | – | 0.32 | 0.24 | 0.25 | 0.23 | 0.25 | 0.23 | 0.23 | 0.25 | 0.26 | 0.29 | – | – |
| F | – | – | – | 0.36 | 0.17 | 0.13 | 0.16 | 0.13 | 0.15 | 0.23 | 0.18 | – | – | – |
| G | – | – | 0.25 | 0.25 | 0.14 | 0.13 | 0.07 | 0.06 | 0.12 | 0.18 | 0.23 | – | – | – |
| H | – | – | – | 0.13 | – | 0.10 | 0.10 | 0.08 | 0.09 | 0.07 | 0.11 | – | – | – |
| I | – | 0.26 | – | 0.20 | 0.17 | 0.12 | 0.12 | 0.12 | 0.13 | 0.17 | 0.13 | 0.25 | – | – |
| x | 0.32 | 0.30 | 0.25 | 0.23 | 0.21 | 0.15 | 0.15 | 0.15 | 0.16 | 0.18 | 0.17 | 0.25 | 0.17 | 0.18 |

**Table 13** Quantitative comparison of *Rhombopora cylindrica* sp. nov. and *Rhombopora hexagona* sp. nov. with some other Carboniferous *Rhombopora* species (dimensions in mm).

| | AR | ZD | Z2 | AD1 | AD2 |
|---|---|---|---|---|---|
| *R. cylindrica* sp. nov. | 10–16 | 0.50–1.10 | 4 | 0.10–0.35 | 0.07–0.18 |
| *R. hexagona* sp. nov. | 9–15 | 0.40–0.90 | 5 | 0.10–0.26 | 0.04–0.18 |
| †*R. ?bifurcata* Campbell, 1961 | – | 1.00–1.60 | – | 0.20–0.23 | 0.10–0.13 |
| *R. nova* Ceretti, 1963 | – | 1.08–1.25 | 3 | 0.38 | 0.16–0.20 |
| *R. multipora* Foerste, 1887 | 20 | 1.40 | 7 | 0.15 | 0.09 |
| *R. prompta* Gorjunova, 1988 | – | 2.52–0.27 | – | 0.30 | 0.20–0.22 |
| *R. johnsvalleyensis* Harlton, 1933 | – | 0.60–0.80 | 5 | 0.19 | 0.10 |
| *R. nitidula* Harlton, 1933 | 6 | 0.4 | 5 | 0.29 | 0.10 |
| *R. millepunctata* McFarlan, 1942 | – | 0.6 | – | 0.14 | 0.06 |
| *R. lepidodendroides* Meek, 1872 | – | 1.00–3.60 | 4 | 0.16–0.29 | 0.09–0.21 |
| *R. ampla* Moore, 1929 | – | 1.00 | – | 0.31 | 0.17 |
| *R. communis* Moore, 1929 | – | 1.00 | 3 | 0.28 | 0.14 |
| *R. constans* Moore, 1929 | 17 | 1.00 | – | 0.29 | 0.14 |
| *R. cortica* Moore, 1929 | – | 1.80–2.70 | 4 | 0.28–0.29 | 0.16–0.17 |
| *R. fovata* Moore, 1929 | – | 1.00–1.15 | – | 0.37 | 0.29 |
| *R. munda* Moore, 1929 | 26 | 1.25 | 3 | 0.33 | 0.18 |
| *R. muralis* Moore, 1929 | – | 1.00 | – | 0.28–0.34 | 0.20–0.25 |
| *R. pilula* Moore, 1929 | 17 | 1.50–1.70 | 4 | 0.43 | 0.26 |
| #*R. tersiensis* Nekhoroshev, 1926 | – | 1.50–2.40 | 5 | 0.16–0.25 | 0.08–0.15 |
| *R. binodata* Trizna, 1958 | – | 1.69–2.00 | 4 | 0.50 | 0.4 |
| *R. floriformis* Trizna, 1958 | – | 1.60–1.70 | 7 | 0.50 | 0.45 |
| *R. insinuata* Trizna, 1958 | – | 1.20–1.40 | 6 | 0.35 | 0.30 |
| *R. novitia* Trizna, 1958 | – | 1.15–1.30 | 5 | 0.30 | 0.25 |
| *R. perpera* Trizna, 1958 | – | 2.00 | 3 | 0.60 | 0.50 |
| *R. sarcinulata* Trizna, 1958 | – | 1.60 | 5 | 0.14–0.15 | 0.08 |
| *R. simplex* Trizna, 1958 | – | 1.10–1.50 | 6 | 0.15 | 0.13 |
| *R. charasensis* Sakagami, 1972 | – | 2.50–3.80 | 5 | 0.19–0.26 | 0.12–0.18 |
| *R. murthyi* Sakagami, 1972 | – | 1.7 | 4 | 0.21–0.3 | 0.10–0.14 |
| *R. diaphragmata* Shulga–Nesterenko, 1955 | – | 2.00–3.00 | 5 | – | – |
| *R. riasanensis* Shulga-Nesterenko, 1955 | – | 0.8 | 4 | – | – |
| *R. variaxis* Shulga-Nesterenko, 1955 | – | 2.00–2.50 | 5 | 0.25 | 0.15 |
| §*R. armata* Ulrich, 1884 | – | 1.00–1.10 | – | – | – |
| *R. crassa* Ulrich, 1884 | – | 2.50–4.50 | 5 | – | – |
| *R. elegantula* Ulrich, 1884 | – | 2.50 | 4 | – | – |
| *R. pulchella* Ulrich, 1884 | – | 0.88 | 4 | – | – |
| *R. incrassata* Ulrich, 1888b | – | 1.00–1.10 | 6 | 0.35 | 0.30 |
| *R. ohioensis* Ulrich, 1888b | – | 1.00–1.30 | – | 0.11–0.25 | 0.07–0.13 |
| *R. angustata* Ulrich, 1890 | 6? | 0.40–0.50 | 4 | 0.17 | 0.08 |
| *R. ?asperula* Ulrich, 1890 | – | 1.00–1.60 | – | – | – |
| *R. attenuata* Ulrich, 1890 | – | 0.70–1.00 | 6 | 0.15 | 0.10 |
| *R. decipiens* Ulrich, 1890 | – | 1.50–3.00 | 11 | 0.15 | 0.10 |
| *R. dichotoma* Ulrich, 1890 | – | 3.00 | 4 | 0.12 | 0.12 |
| *R. exigua* Ulrich, 1890 | – | 0.60–0.80 | – | 0.11 | – |
| *R. gracilis* Ulrich, 1890 | – | 1.30 | 7 | 0.10 | – |
| *R. minor* Ulrich, 1890 | – | 0.50–0.90 | – | 0.12 | – |
| *R. nickesi* Ulrich, 1890 | – | 0.40–0.90 | – | 0.17 | – |
| *R. simulatrix* Ulrich, 1890 | – | 1.00–2.10 | 6 | 0.12 | – |
| *R. ?spiralis* Ulrich, 1890 | – | 1.50–2.00 | 5 | 0.21 | – |
| *R. tabulata* Ulrich, 1890 | – | 1.00–1.50 | 5 | 0.18 | 0.12 |
| *R. tenuirama* Ulrich, 1890 | 10 | 0.40–0.50 | 5 | 0.11 | 0.08 |
| *R. transversalis* Ulrich, 1890 | – | 2.50–4.00 | 5 | 0.12 | – |
| *R. varians* Ulrich, 1890 | – | 2.00–4.00 | 7 | 0.12–0.13 | – |
| *R. pseudonovita* Yang & Lu, 1962 | – | 1.10–1.70 | 6 | 0.12–0.20 | 0.07–0.11 |
| *R. staffordotaxiformis* Yang *et al.*, 1988 | – | 1.14–1.53 | 4 | 0.16–0.21 | 0.07–0.10 |

Dimensions condensed from primary sources except where indicated:
†: Sabattini, 1972; *: Huffman, 1970; #: Sakagami, 1972; §: Ulrich, 1890; †: Lu, 1989.

DISTRIBUTION. Carrick Lough, County Fermanagh, and Hook Head, County Wexford.

Family **HYPHASMOPORIDAE** Vine, 1885
Genus ***STREBLOTRYPA*** (Ulrich MS.) Vine 1884b

TYPE SPECIES. *Streblotrypa nicklesi* (Ulrich MS.) Vine, 1884b, by monotypy, from the Lower Carboniferous of Hurst, Yorkshire, England and Illinois, U.S.A.

TYPES. Duncan (1949) has discussed the problem of Vine's lost material and the implications for the type specimens. She designated a suite of specimens collected by Ulrich in North America (USNM 43311) as (neo)types. Indeed, she should have only designated *one* neotype. Hageman (1993) has designed one of Ulrich's syntypes (USNM 114392) as the neotype.

DISCUSSION. Confusion has existed over the authorship and the concept of the type species of the genus. J.M. Nickles of the U.S. Geological Survey sent specimens of a bryozoan from the Carbon-

iferous of Kaskasia, Illinois to Vine and Ulrich in 1883. Ulrich, in an 1884 manuscript, named them *Streblotrypa nicklesi* and this description subsequently appeared in print (Ulrich 1890: 667). However, before the appearence of Ulrich's paper, Vine (1884b: 391) published a description of the American specimens together with some specimens from Yorkshire and named them as *S. nicklesi*, stating that this was the name used by Ulrich in his manuscript which as such 'had no validity'. Yet in his subsequent papers Vine (1885, 1889) credits the genus and species, which he consistently names as *nicklesi*, to Ulrich. As was clear later Ulrich had in fact named the taxon *S. nicklesi*, and Hageman (1993) has corrected Vine's error and quotes Ulrich's spelling as the correct name of the type species, and credits Ulrich in Vine as the author. *S. minuta*, described as a new variety by Vine in 1885, was later considered by him to be a variety of *S. 'nicklesi'* (Vine, 1889).

Unfortunately, Vine's original specimens are lost, and it is possible that the American and English forms are not conspecific. Therefore, what is now in question is the original concept of the species and the validity of Hageman's designation of the neotype: should the concept be based upon the American specimens (as is generally agreed (Blake 1983)) or on the now missing British specimen? If it is shown that the original material belonged to two separate taxa then perhaps either the American or British material needs renaming. New collecting is needed at Vine's original locality at Hurst, north Yorkshire, which may yield specimens of *Streblotrypa*, so that comparison with the American material can be made.

Subgenus ***STREBLOTRYPA (STREBLOTRYPA)*** (Ulrich MS.) Vine 1884b

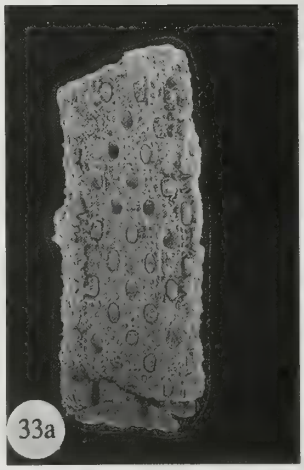
DISCUSSION. Blake (1983: 590) recognized two subgenera in *Streblotrypa*: *S. (Streblotrypa)* and *S. (Streblascopora)* Bassler, 1952. This differentiation is based on the number of axial zooecia contained in the endozone, the location of metapores between autozooecial apertures, and the presence or absence of hemisepta. Species of *S. (Streblascopora)* display a distinct axial area with more than 10 axial zooecia. Metapores are frequently found beyond the lateral margins of autozooecia, and hemisepta are rare or absent. The opposite holds for *S. (Streblotrypa)*.

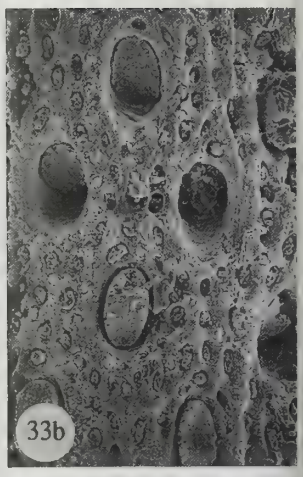
***Streblotrypa (S.) pectinata*** Owen, 1966 Figs 33–36

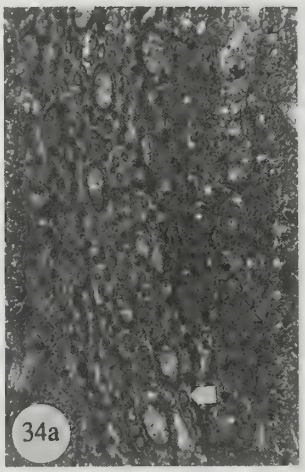
v1966 *Streblotrypa pectinata* Owen: 144, pl.10, figs A–C.

MATERIAL. BMNH PD9565-9579; TCD.34049, 34124, 34129, 34130, 34140; BELUM K3239, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42529-42530, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoarium ramose and composed of cylindrical branches 0.67 to 1.04mm in diameter with a circular cross-section.







**Figs 33–35** *Streblotrypa pectinata* Owen, 1966; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. **33,** BMNH PD9565; **33a,** zoarial fragment showing dendroid colony form, oval-shaped autozooecial apertures arranged in longitudinal rows, with three to four rows of metapores developed between, ×35; **33b,** detail of 33a, ×150. **34,** BMNH PD9578; **34a**, tangential section showing autozooecial apertures surrounded by small metapores (arrowed), ×100; **34b**, detail of 34a, ×100. **35,** BMNH PD9579; **35a**, longitudinal section showing thin exozone pierced by acanthostyles, ×30; **35b**, detail of 35a showing acanthostyles in exozonal wall – the calcite rods clearly deflect the skeletal laminae of the outer wall, ×100.

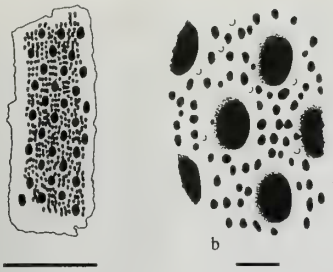



**Fig. 36** Line drawing of external features of *Streblotrypa pectinata* Owen, 1966 (BMNH PD9565); **a,** colony form, scale bar = 1 mm; **b,** detail of autozooecial apertures surrounded by metapores, scale bar = 0.1 mm.

No complete colonies were observed; the largest fragment examined measured 10.2mm in length. Branches bifurcate at irregular intervals, and lateral ramifications diverge at a high angle of between 83° and 90°. Branches retain a constant width between ramifications and there is only a slight increase just prior to and after branching.

Autozooecial apertures are moderate in size (0.08–0.19 by 0.05–0.10mm), oval in shape, evenly spaced 2 to 2.5 diameters apart, and occur in 12 to 20 longitudinal rows around the entire branch. Within any one zoarial fragment apertures are of approximately constant dimension. Small oval to occasionally circular-shaped metapores are abundant; twelve to twenty occur in 3 to 4 longitudinal rows between the distal and proximal extremities of adjacent autozooecial apertures, and beyond the lateral margins either a single or double row of metapores is present. In cross-section metapores have a thin neck and flare towards the endozone. They are approximately 0.09mm deep; only a small proportion of metapores penetrate to the base of the exozone.

Autozooecia are budded from an axial region in which axial zooecia are not present. Chambers are initally recumbent in the endozone and diverge from the branch axis at a low angle of less than 25°. At the exozone they bend through 65° to become orientated nearly perpendicular to the zoarial surface. From this surface the proximal wall of the vestibule slopes at a moderate angle, while the distal wall is perpendicular (Fig. 35a). In cross-section chambers are pentagonal and slightly inflated laterally. Chamber walls in the endozone are thin (0.01mm) and composed of a granular core covered with very thin laminated layers. The walls thicken rapidly intrazooidaly (up to 0.4mm) in the exozone; much of this expansion is due to metapore development.

Acanthostyles are small (0.02–0.05mm in diameter) and blunt and are randomly distributed in interapertural areas where they lie at the proximal end of metapores. Acanthostyles arise at the endozone/exozone boundary, thicken slightly laterally and have solid cores composed of granular skeleton, around which is bent laminated skeleton. They form dark granular circles on the zoarial surface.

**Table 14** Measurements of *Streblotrypa pectinata* in mm. N=13.

| | MN | x | Mn | Mx | CV | wCVb |
|---|---|---|---|---|---|---|
| D | 95 | 0.87 | 0.67 | 1.04 | 3.84 | 8.75 |
| 2 | 33 | 6.08 | 6 | 7 | 1.48 | 29.80 |
| D1 | 114 | 0.11 | 0.08 | 0.19 | 11.05 | 8.76 |
| D2 | 113 | 0.07 | 0.05 | 0.10 | 13.90 | 5.16 |
| S | 193 | 0.34 | 0.30 | 0.51 | 6.50 | 12.92 |
| ID | 76 | 0.02 | 0.01 | 0.05 | 26.25 | 3.96 |
| T | 24 | 0.56 | 0.41 | 0.80 | 10.06 | 6.25 |
| E | 32 | 0.13 | 0.08 | 0.22 | 16.49 | 3.87 |
| H | 16 | 0.03 | 0.02 | 0.06 | 17.15 | 2.53 |
| T | 45 | 0.02 | 0.02 | 0.05 | 18.86 | 3.51 |

DISCUSSION. *Streblotrypa pectinata* is very rare in the Lower Carboniferous of the British Isles. From the limestones of County Fermanagh less than 20 zoarial fragments and a small number of specimens in section were found.

The presence of metapores, small acanthostyles, and a thin exozone make this bryozoan very distinctive. Only three other species of *Streblotrypa* have been described from strata of Carboniferous age in the British Isles: *Streblotrypa cortacea* (Owen 1966), *Streblotrypa minuta* (Vine 1889), and *Streblotrypa nicklesi* (Ulrich *in* Vine 1884b). *S. pectinata* differs from *S. cortacea* which possesses a thick exozone and few metapores; *S. minuta*, in which sharp longitudinal ridges and a small number (6 to 8) of metapores are developed; and *S. nicklesi*, which has 9 to 15 metapores and 12 longitudinal rows of autozooecial apertures.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian).

DISTRIBUTION. Apart from the occurrences at Carrick Lough and Sillees River, County Fermanagh *Streblotrypa pectinata* has previously only been recorded from Castleton, Derbyshire (the type locality).

## Genus ***CLAUSOTRYPA*** Bassler, 1929

TYPE SPECIES. *Clausotrypa separata* Bassler, 1929 by original designation from the Permian of Timor.

DISCUSSION. The taxon has both trepostome and cryptostome features. Of the former the long autozooecial chambers, moderately thick exozone, many acanthostyles particularly associated with autozooecial apertures. The dendroid zoarial form, arrangement of autozooecial apertures and the presence of metapores strongly suggest cryptostome affinities. I consider *Clausotrypa* to have stronger cryptostome than trepostome affinities.

Bassler (1929) assigned the genus to the Order Cryptostomata, family Rhabdomesidae. Many Soviet authors have placed it in the suborder Rhabdomesina Astrova & Morozova, 1956 (Romantchuk 1970, Morozova 1970, 1981), while others assign the genus to the suborder Streblotrypina Gorjunova, 1985 (Gorjunova 1985). Blake (1983: 592) does not consider *Clausotrypa* to be a rhabdomesonid, while Gorjunova (1985) does. Blake & Snyder (1987) show, based on a cluster analysis of 44 characters, that *Clausotrypa* is rather unusual. It does not easily fall into any familial grouping.

Recognising the obvious need for fuller taxonomic and comparative studies the genus is tentatively placed here in the family Hyphasmoporidae, Vine 1885.

### ***Clausotrypa ramosa*** (Owen, 1973) comb. nov. Figs 37–41

v1973 *Sulcoretepora? ramosa* Owen: 304, pl. 9a–c.

HOLOTYPE. The holotype of *Sulcoretepora? ramosa* Owen, 1973 is represented by a zoarial fragment and three thin sections cut from it, collected from shales below the Rossmore Mudstone (upper Viséan), Tullaghoge, County Tyrone, in the collections of the Ulster Museum (BELUM K1830).

MATERIAL. BMNH PD9577; 9627-9637; 9730-9739; TCD.34067-34078, 34136, 34163, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42513, 42531-42534, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DIAGNOSIS. *Clausotrypa* forming semi-robust erect cylindrical dichotomising zoaria. Autozooecia more frequent on one side of branch than the other. Metapores, closed to the surface, are developed in interapertural areas. Autozooecial apertures are circular, moderate in size, widely spaced, and are surrounded by six to eight

acanthostyles. Strong undulating ridges and short acanthostyles are common in interapertural areas.

DESCRIPTION. Zoaria form dendroid expansions of unknown maximum height and are composed of cylindrical dichotomising or bifurcating branches 0.46 mm to 1.12 mm in diameter.

Autozooecia are arranged in poorly defined longitudinal rows and are developed throughout the zoarium. They are budded from a central undulating axis in an annular or irregular pattern. Autozooecial chambers have a sub-linear shape, are eight times as long as wide, and diverge distally from the axis at low angles of between 10° and 20°. They bend slightly at the exozone and vestibules are orientated at a high angle to the zoarial surface. In cross-section chambers are sub-rounded in shape. Endozonal walls are thin, undulatory, and retain a constant width along their length. Chamber walls are thickened in the exozone to a maximum width of 0.52 mm. The exozone averages 0.07 mm in width and is approximately one sixth of the branch diameter on either margin.

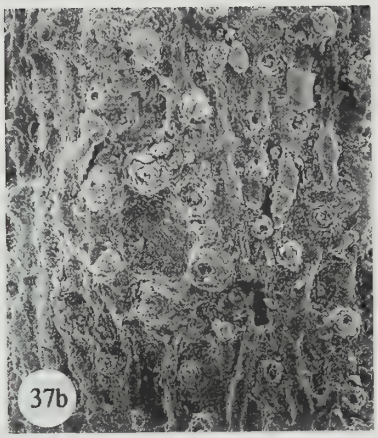
Metapores are developed at the top of the endozone and the base of the exozone. They are small, circular to oval structures, usually closed at the zoarial surface. One or two are disposed between autozooecia.

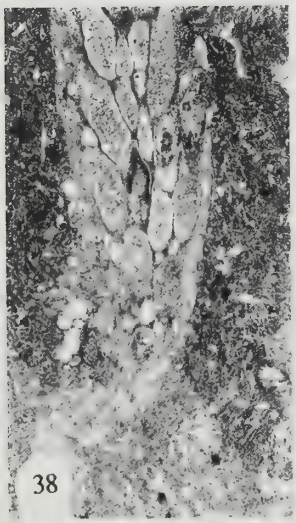
Autozooecial apertures are moderate in size, oval in shape, widely spaced approximately four to five diameters apart, and are arranged in longitudinal rows around branches. On most zoaria apertures are more abundant on one side of branches than on the other.

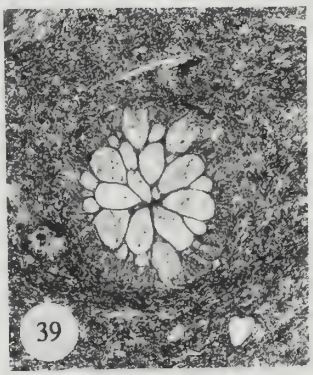
Acanthostyles are common. Six to ten surround autozooecial apertures, often resembling a peristome, and they also occur randomly and widely scattered in interapertural areas. They develop from the base of the exozone only. Strong longitudinal ridges also decorate interapertural areas.

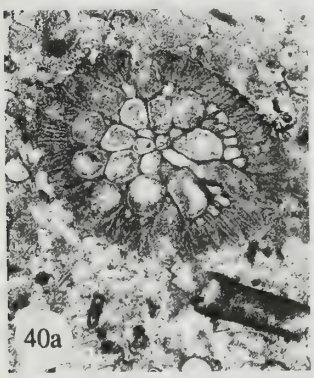
DISCUSSION. *Clausotrypa ramosa* was first described as *Sulcoretepora? ramosa* by Owen (1973: 305). He suggested that the taxon is either a sulcoreteporid or a rhabdomesonid depending on which of the two characters, the presence of mesozooecia ('mesopores' of Owen), or the ramose zoarial form, is considered to be of stronger generic importance. He assigned the taxon to the former, but ignored the diagnostic features of the genus *Sulcoretepora*, namely the bifoliate zoarial habit and the arrangement of autozooecia in longitudinal rows, budded from a plicated median carina.

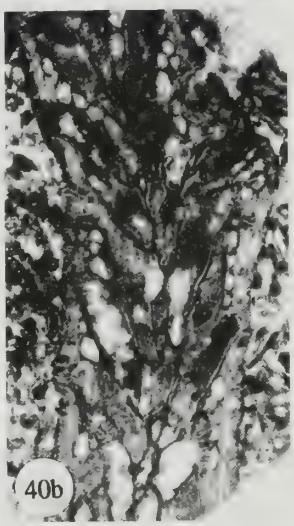
Several *Clausotrypa* species have been previously described. Of


**Figs 37–40** *Clausotrypa ramosa* (Owen, 1973) comb. nov.; **37–39**; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. **37,** BMNH PD9627; **37a,** dendroid zoarium showing aborted lateral branch development, oval-shaped autozooecial apertures arranged in crude longitudinal rows, with striated ridged interapertural areas, ×25; **37b,** detail of 37a, showing oval-shaped autozooecial aperture surrounded by seven large acanthostyles. Acanthostyles are also developed in interapertural areas, ×200. **38,** BMNH PD9636, longitudinal section showing sublinear autozooecial chambers, budded from a poorly defined axis. Circular metapores are present at the endozone/exozone boundary, ×25. **39,** BMNH PD9637, transverse section showing pyriform autozooecial chamber cross-sections, circular/polygonal metapores, and acanthostyles in exozone, ×25. **40,** Limestone and Shales below Rossmore Mudstone (Upper Viséan), Tullaghoge, County Tyrone; Owen Collection. BELUM K.183( **(lectotype)**; **40a**, transverse section showing pyriform autozooecial chamber cross-sections, and circular/polygonal metapores (figured as *Sulcoretepora ramosa* by Owen, 1973, pl. 9c, ×25); **40b**, longitudinal section showing autozooecial chambers budded from an irregular axis, and small circular/polygonal metapores developed at the base of the thi exozone region (figured as *Sulcoretepora ramosa* by Owen, 1973, pl. 9b, ×25).

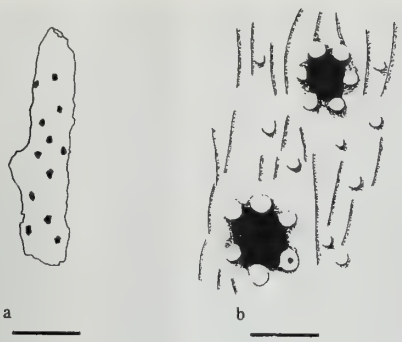



**Fig. 41** *Clausotrypa ramosa* (Owen, 1973) comb. nov. Line drawing of external features of BMNH PD9627; **a,** colony form, scale bar = 1 mm; **b,** detail of autozooecial apertures; scale bar = 0.1 mm.

**Table 15** Measurements on *Clausotrypa ramosa* (in mm). N=17.

| | MN | x | Mn | Mx | CV | wCVb |
|---|---|---|---|---|---|---|
| ZD | 102 | 0.73 | 0.46 | 1.12 | 7.56 | 5.97 |
| AD1 | 107 | 0.11 | 0.06 | 0.16 | 13.06 | 9.68 |
| AD2 | 106 | 0.08 | 0.05 | 0.14 | 14.87 | 7.67 |
| WT1 | 57 | 0.53 | 0.28 | 0.85 | 12.85 | 4.14 |
| WT2 | 64 | 0.25 | 0.15 | 0.42 | 17.38 | 4.38 |
| Z2 | 13 | 3.4 | 2 | 5 | 16.05 | 3.9 |
| ET | 6 | 0.42 | 0.31 | 0.52 | 10.60 | 4.34 |
| TE | 10 | 0.07 | 0.03 | 0.17 | 14.54 | 1.33 |

these only one, *C. limpida* Gorjunova, 1988, is from the Carboniferous, while all the rest occur in Permian strata. Comparison of *C. ramosa* with these species shows it to be distinct from them all (see Table 16). It is morphologically most similar to *C. monticula* (Eichwald, 1860) but differs significantly by having thicker branches and larger autozooecial apertures. Bassler (1929) regards *Rhombopora? spiralis* Ulrich 1890 from the Carboniferous of Kentucky as belonging to *Clausotrypa*. However, after examination of the original description and figures I consider the taxon to be correctly identified by Ulrich.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian).

DISTRIBUTION. Carrick Lough and Sillees River, County Fermanagh and Tullaghoge, County Tyrone, Ireland.

Order **FENESTRATA** Elias & Condra, 1957
Family **ACANTHOCLADIIDAE** Zittel, 1880
Genus ***BACULOPORA*** Wyse Jackson, 1988

TYPE SPECIES. *Vincularia megastoma* M'Coy, 1844 by original designation, from the Lower Carboniferous (Viséan, Brigantian) of Killymeal, Dungannon, County Tyrone, Ireland.

***Baculopora megastoma*** (M'Coy, 1844) Fig. 43

MATERIAL. BMNH PD8109-PD8127, TCD.29284-29303, TCD.34124, 34131, 34156, 34162; NMI: F19501-F19520; BELUM K3137, K3436, K12088-K12107, Upper part of the Glencar Limestone, Viséan (Asbian), Carrick Lough, County Fermanagh. BMNH PD8128-PD8132; TCD.42535-42538, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

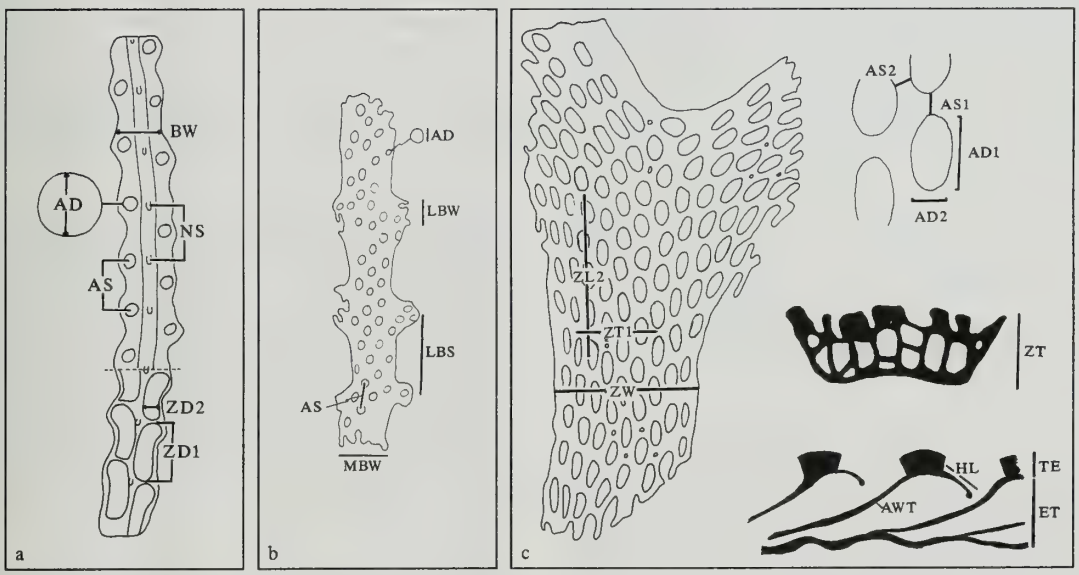



**Fig. 42** Measurements taken on fenestrates in this study. **a,** *Diploporaria tenella*; **b,** *Ichthyorachis newenhami*; **c,** *Rhombocladia dichotoma*. AD = Autozooecia apertural diameter; AD1 = Autozooecia apertural diameter measured parallel to growth direction; AD2 = Autozooecia apertural diameter measured perpindicular to growth direction; AR = Number of longitudinal autozooecial rows; AS = Autozooecia apertural spacing: minimum distance between two adjacent autozooecial apertures, measured from their centres; AS1 = Autozooecia apertural spacing measured parallel to growth direction; AS2 = Autozooecia apertural spacing measured perpendicular to growth direction; AWT = Autozooecial chamber wall thickness; BW = Branch width; ET = Endozone thickness; HL = Hemiseptum length; LBW = Lateral branch width measured perpendicular to growth direction; LBS = Spacing between the centres of two successive lateral branches; MBW = Main branch width measured perpendicular to growth direction; NS = Nodal spacing: distance between two adjacent carinal nodes; TE = Exozone thickness; ZD1 = Length of autozooecial chamber; ZD2 = Width of autozooecial chamber; ZL2 = Number of autozooecial apertures contained in a 2mm line drawn parallel to growth direction; ZT = Zoarial thickness; ZT1 = Number of autozooecial apertures contained in a 1mm line drawn perpendicular to growth direction; ZW = Zoarial width.

**Table 16** Comparison of *Clausotrypa* species (dimensions in mm).

| | ZD | AD1 | AD2 | IWT1 | IWT2 |
|---|---|---|---|---|---|
| *C. ramosa* (Owen, 1973) comb. nov. | 0.46–1.12 | 0.06–0.16 | 0.05–0.14 | 0.28–0.85 | 0.15–0.42 |
| *C. limpida* Gorjunova, 1988 | 0.6–0.9 | 0.25 | 0.13 | | – – |
| *C. clara* Krutchinina, 1986 | 2.5–3.0 | 0.4–0.5 | 0.2–0.25 | 0.2 | 0.12 |
| *C. conferata* Bassler, 1929 | 2.8 | 0.32 | 0.25 | 0.2 | 0.1–0.15 |
| *C. costata* Romantchuk, 1981 | 4.2–4.3 | 0.21 | 0.16–0.2 | 0.3–0.6 | 0.43–0.64 |
| *C. exillis* Sakagami, 1961 | 1.3–1.4 | 0.1–0.13 | – | – | – |
| *C. minor* Bassler, 1929 | 1.3 | 0.2–0.25 | 0.15–0.20 | 1.0 | 0.3 |
| *C. monstruosa* Morozova, 1970 | 4.0–4.5 | 0.16–0.2 | – | – | – |
| *C. monticola* (Eichwald, 1860) | 1.0–2.5 | 0.17–0.2 | 0.12–0.14 | – | – |
| *C. petaloides* Romantchuk, 1970 | 4.8–5.0 | 0.24–0.25 | – | – | – |
| *C. separata* Bassler, 1929 | 0.15–2.6 | 0.3 | 0.17 | 0.4 | 0.3 |
| *C. spinosa* Fritz, 1932 | 1.0–1.5 | 0.26–0.27 | 0.13–0.14 | 0.35 | 0.3 |

Data from original sources.

DESCRIPTION. Colonies consist of very slender branches that divide at irregularly spaced intervals, with branches bifurcating at low angles, and with lateral ramifications also occurring. Branches are straight or gently flexous, and are circular in cross-section. No complete colonies have been discovered, and the largest fragment examined was 1.53mm in length. Bifurcations and lateral branches appear to be widely spaced, as two laterals have not been observed on the same colony. Distal branches are thinner than proximal branches, with a range in diameter from 0.26mm to 0.36mm observed in one colony fragment. Branch width decreases slightly after bifurcation but soon increases to equal the width of the preceeding link. Lateral branches are thinner than main branches. The obverse surface bears faint undulating striae, occasionally with rows of small circular stylets (weathering to small pits) along the crests of striae.

Autozooecial apertures are regularly arranged in quincunx, in four to seven longitudinal rows. They are small, circular, lack peristomes and are evenly spaced along the length of the branch. Some apertures are surrounded by six small pustules, giving them a stellate appearance. The reverse surface is smooth or faintly striated. Autozooecial chambers are rectangular in profile with pentagonal bases.

Internally the skeletal arrangement is tripartite; a primary granular layer is surrounded by an inner laminated layer lining zooecial chambers, and an outer laminated layer. Small stylets composed of granular skeleton penetrate through the outer laminated skeleton where they appear as pustules or weathered pits.

DISCUSSION. A complete systematic description of the genus *Baculopora* and the species *B. megastoma* is given in Wyse Jackson (1988).

## Genus ***DIPLOPORARIA*** Nickles & Bassler, 1900

TYPE SPECIES. *Glauconome (Diplopora) marginalis* Young & Young, 1875, by original designation from the Upper Limestone Shales (Lower Carboniferous) of the British Isles (cited localities: Hairmyres, East Kilbride; Beghill, near Hamilton; Gillfoot, near Carluke; Hook Head, County Wexford).

### ***Diploporaria marginalis*** (Young & Young, 1875)

Figs 44, 49

1875 *Glauconome (Diplopora) marginalis* Young & Young: 326, pl.3, figs 14–21.
1877 *Glauconome (Diplopora) marginalis* Young & Young; Vine, fig. 207.
1881 *Glauconome (Diplopora) marginalis* Young & Young; Vine: 333.
1885 *Diplopora marginalis* Young & Young; Vine: 83.
1900 *Diploporaria marginalis* (Young & Young); Nickles & Bassler: 233.
1953 *Diploporaria marginalis* (Young & Young); Bassler: G127, figs 87 – 6a, 6b.
1975 *Diploporaria marginalis* (Young & Young); Graham: 9, pl. 4, figs 6, 6a, 6b.
1987 *Diploporaria marginalis* (Young & Young); Bancroft: 196.
1991 *Diploporaria marginalis* (Young & Young); Billing: 41.

LECTOTYPE. Graham (1975) designated a lectotype but cited a cavity slide that contained several zoaria. Consequently Bancroft (1984-ms) designated specimen number 14 in cavity slide HM D144 (Hunterian Museum) as lectotype. This designation is formalised herein.

MATERIAL. Three zoarial fragments, BMNH PD9580;TCD.34050-34051, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

DESCRIPTION. Zoaria are small non-pinnate expansions, composed of delicate straight branches 0.21 to 0.34 mm in diameter with sub-circular cross-sections. Lateral branches were not developed in the specimen examined.

Autozooecia are arranged in two longitudinal rows along the length of the branch. Autozooecial apertures are small (0.07–0.09 mm in diameter), circular, and are surrounded by a complete peristome. They are regularly spaced two to two and a half diameters apart either side of a median carina. The lateral margin and up to half the apertural diameter protrudes beyond the margin of the branch. This produces a sharp serrated branch outline.

A faint median carina carries regularly spaced oval to circular nodes 0.02 mm in diameter. Two equally faint longitudinal ridges lie either side of the median carina inside the inner margins of autozooecial apertures. Interapertural areas are smooth. The reverse surface is gently rounded and smooth. Internal features were not seen.

**Table 17** Measurements of *Diploporaria marginalis* (in mm). N=1.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW | 10 | 0.27 | 0.21 | 0.34 | 4.40 | – |
| AD | 10 | 0.08 | 0.07 | 0.09 | 10.52 | – |
| AS | 11 | 0.29 | 0.28 | 0.33 | 28.85 | – |
| NS | 6 | 0.30 | 0.28 | 0.32 | 22.69 | – |

DISCUSSION. *Diploporaria marginalis* is very rare in the Asbian of County Fermanagh. In the present study only three zoarial frag

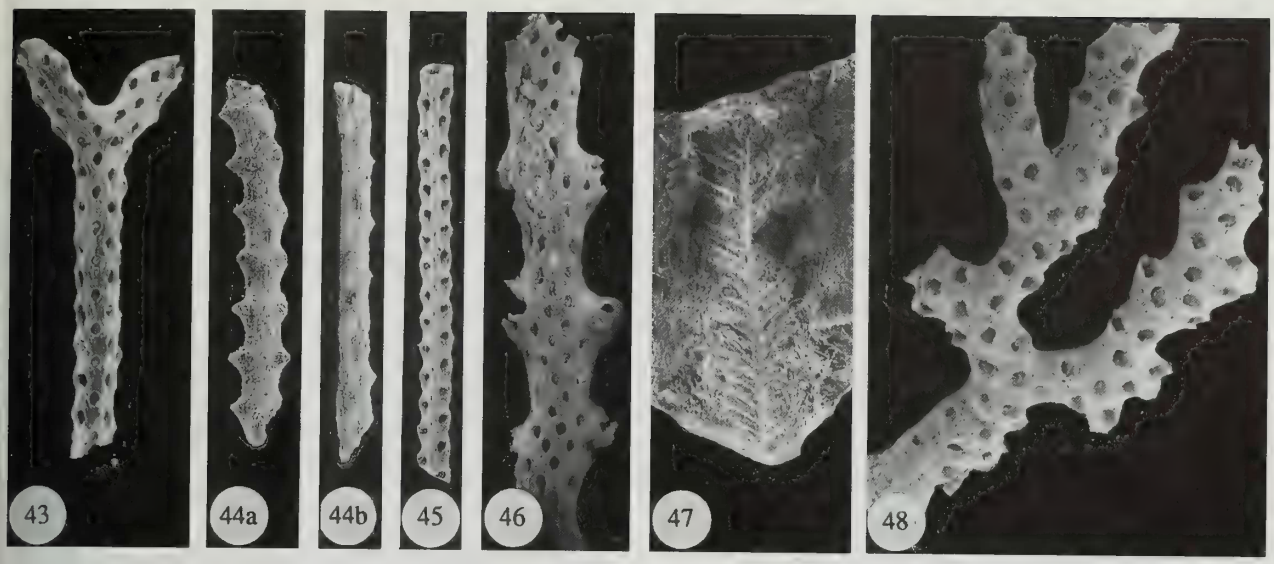



**Fig. 43** *Baculopora megastoma* (M'Coy, 1844); Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. BMNH PD8109, obverse surface detail with five longitudinal rows of autozooecia and bifurcation of zoarium, ×22.

**Fig. 44** *Diploporaria marginalis* (Young & Young, 1875); Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. BMNH PD9580; **44a,** obverse surface of branch fragment showing disposition of autozooecia in two longitudinal rows, one either side of a strong median carina. The carina consists of adjacent longitudinal ridges, the central one of which bears distinct nodes. Autozooecial apertures are circular and their edges protrude far beyond the branch margin, ×40; **44b,** lateral view showing elevated carinal nodes, ×40.

**Fig. 45** *Diploporaria tenella* Wyse Jackson, 1988; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. BMNH PD8138 **(holotype)**, obverse surface detail of a slender zoarium with one row of autozooecial apertures developed either side of a central carinal ridge, ×25.

**Figs 46–47** *Ichthyorachis newenhami* M'Coy, 1844; **46,** Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. BMNH PD9581, obverse surface showing a strong mainstem and broken lateral branches. Four longitudinal rows of autozooecia are developed on the former, fewer rows on the latter. Autozooecial apertures are small and circular in shape, ×20. **47,** Carboniferous Limestone (Dinantian), Kilmallock, County Limerick. NMING:F6044 **(lectotype)**, large colony fragment consisting of a straight mainstem with straight lateral branches diverging at moderate angles. Preservation of the specimen is poor and autozooecia of the mainstem are not seen; some lateral branches carry four autozooecial rows. Figured by M'Coy, 1844, pl. 29, fig. 8, ×0.8.

**Fig. 48** *Thamniscus colei* Wyse Jackson, 1988; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. BMNH PD8959 **(holotype)**, obverse surface detail showing circular bifurcating branches, autozooecia developed in three to four irregular rows, and circular apertures surrounded by complete peristomes, ×20.

ments were recovered. *D. marginalis* is a distinct species which can easily be recognised from its delicate zoarium with strongly serrated margins caused by autozooecial apertures that project laterally.

It was first described as a *Glauconome* species by Young & Young 1875). They noted the presence of small orifices proximal to autozooecial apertures which were divided from them by a thin septum. Abrasion of this septum produced a pyriform aperture. Such apertures and 'orifices' have not been observed by subsequent workers. They probably result from the abrasion of the zoarial surface and the revealing of the superior hemiseptum (Ulrich 1890, Bancroft 1984).

Vine (1881, 1885) added nothing to the original description of the species. He refers to a more robust form found in Scotland. However, as he does not illustrate these forms, and as his specimens are lost it is impossible to substantiate these records.

While the two species of *Diploporaria* found in the British Isles (*D. marginalis* and *D. tenella*) show morphological similarities there are a number of important differences between them. The autozooecial apertures in *D. marginalis* possess a prominent outer peristomial rim which extends markedly beyond branch margins giving branches a strongly serrated outline. In *D. tenella* peristomial rims are absent and autozooecial apertures hardly protrude beyond the branch margins giving them a smooth sinuous outline. Apertures are generally spaced further apart in *D. tenella*. Carinal nodes in *D. tenella* are more evenly and closely spaced than in *D. marginalis*.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian-Brigantian). The range has been extended downwards into the Asbian for the first time.

DISTRIBUTION. This is the first record of this species outside Great Britain where it is common in the Midland Valley of Scotland and rarer in Yorkshire and Lancashire. It is very rare in County Fermanagh.

### *Diploporaria tenella* Wyse Jackson, 1988. Figs 42a, 45

MATERIAL. BMNH PD8138-PD8149, PD8950-8958, TCD.29303-29313, TCD.34132; NMI:F19521-F19530, BELUM K12108-K12117, Upper part of the Glencar Limestone, Viséan (Asbian), Carrick Lough, County Fermanagh. TCD.42539-42542, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Colonies are very small and branches dichotomise irregularly. The largest fragment examined measured 5.9mm in length. Branches are slender, gently flexuous, and have a sub-circular cross-section. Lateral branches diverge at angles of between 70° to 80° from the main stem and slight flaring of lateral branch bases accompanies their development. Branch surfaces are smooth

to faintly pustulose. A narrow but prominent median carina is developed on the mainstem and lateral branches, and distinct nodes are regularly spaced on the carina at distances equal to the interapertural spacing.

Autozooecial apertures are small, circular, and lack peristomial rims. They are regularly spaced (about twice their diameter apart) and are usually alternately arranged in two longitudinal rows on either side of the median carina, but may occasionally may be paired across the carina. The outer margins of autozooecial apertures protrude slightly beyond the lateral margin of branches, producing a gently sinuous branch outline. Internally the chambers are pentagonal in transverse section and longitudinally rectangular. Hemisepta are not developed.

DISCUSSION. A complete systematic description of *D. tenella* is given in Wyse Jackson, 1988.

## Genus *ICHTHYORACHIS* M'Coy, 1844

TYPE SPECIES. *Ichthyorachis newenhami* M'Coy, 1844, by monotypy, from the Lower Carboniferous (Viséan, Chadian?) of Killmallock, County Limerick, Ireland.

M'COY'S ORIGINAL DIAGNOSIS. 'Coral plumose, composed of a straight, central stem or midrib, having on either side a row of short, simple branches or pinnae, all in the same plane; obverse both of the midrib and lateral branches rounded, without keel, and each bearing several rows of small, prominent, oval pores, arranged in quincunx; reverse rounded, smooth or finely striated.'

EMENDED DIAGNOSIS. Acanthocladiid with pinnate zoarium composed of a mainstem and regularly-spaced, co-planar lateral branches which diverge from the mainstem at a high angle. Dissepiments are absent. Branches are circular to sub-circular in cross-section. Interapertural areas and the branch reverse surface are smooth or faintly striated. Autozooecia are arranged in 4 to 6 longitudinal rows on the mainstem, and in 3 to 4 rows on lateral branches. Autozooecial apertures are small, circular to oval in shape, regularly-spaced, and occur on the obverse surface only.

STRATIGRAPHICAL RANGE. Lower Devonian–Lower Carboniferous.

DISTRIBUTION. British Isles, Europe, United States.

### *Ichthyorachis newenhami* M'Coy, 1844

Figs 42b, 46–47, 51

v1844 *Ichthyorachis newenhami* M'Coy: 205, pl.29, fig.8.
1854b *Ichthyorachis newenhami* M'Coy; M'Coy: 104.
1857 *Ichthyorachis newenhami* M'Coy; Jukes: 454.
1862 *Icthyorachis* [sic] *newenhami* M'Coy; M'Coy, pl.29, fig.8.
1883 *Ichthyorachis* sp. Vine: 171.
1884a *Ichthyorachis newenhami* M'Coy; Vine: 196.
1886 *Ichthyorhachis* [sic] *nevenhami* [sic] M'Coy; Hoernes: 230, fig. 233.
1953 *Ichthyorachis newenhami* M'Coy; Bassler: G128, fig. 88 (3a–c).
1966v *Penniretepora triserialis* Owen: 141, pl.9, figs A–C *pro parte.*

LECTOTYPE. Herein designated NMING:F6044; Kilmallock, County Limerick (Viséan, Chadian?); C.B. Newenham Collection; figured M'Coy 1844, pl.29, fig.8. This is the only extant specimen of *Ichthyorachis* from the collection on which M'Coy based his description. Newenham also collected specimens from County Cork (M'Coy 1844: 206).

MATERIAL. BMNH PD9581-9590, TCD.34052, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

M'COY'S ORIGINAL DIAGNOSIS. 'Stem and lateral branches with five rows of oval, prominent pores, closely arranged in quincunx; reverse flattened, slightly convex, divided by a deep groove along the middle; obsoletely striated longitudinally; lateral branches half the thickness of the midrib, space between them equal to the diameter of the midrib.'

EMENDED DIAGNOSIS. *Ichthyorachis* with small delicate pinnate zoaria. Two sets of straight lateral branches diverge from either side of a thin, straight central main stem at a high angle. Lateral branches are regularly spaced and may be offset from each other either side of the main stem, but more frequently occur paired. Branches are circular to subcircular in cross-section. The obverse surface is smooth and rounded, with faint longitudinal striae in interapertural areas. The reverse surface is barren, rounded or slightly flattened; smooth, longitudinally striated, or with a central groove occurring down the centre. Autozooecia are arranged in longitudinal rows on branches with 4 to 5 on the main stem and 3 to 4 on laterals.

Autozooecial apertures are small, circular to oval in shape, lack peristomes, and are regularly arranged in quincunx.

DESCRIPTION. Zoaria form small pinnate expansions, consisting of a main stem and lateral branches. The largest fragment in the County Fermanagh assemblage examined is 17.3 mm in length (the lectotype, which was collected in County Limerick, is larger, and measures 53 mm in length (Fig. 47)). The main stem is thin, straight or gently flexuous, and circular in cross-section. A small increase in main stem diameter precedes lateral branch development. Lateral branches lie in the same plane as the mainstem, and branch from it at angles of between 50° and 60°. They are regularly spaced, about 2 diameters apart, and usually paired either side of the main stem. Occasionally they are marginally offset. Lateral branches are thinner than the mainstem with a straight or undulatory margin, and circular cross-section. The longest lateral branch observed is only 1 mm in length: most are broken at their bases. The obverse surface is rounded and faint longitudinal striae are developed along its length. The reverse surface is also rounded, and may bear indistinct longitudinal ridges or be smooth.

Autozooecia are arranged regularly in 4 to 5 longitudinal rows on the main stem, and 3 to 4 rows on the lateral branches. Autozooecial apertures are small, circular, and constantly spaced about 2 diameters apart. Apertural spacing becomes fractionally closer towards branch node.

Details of internal features are unknown as only silicified fragments have been recovered from Carrick Lough.

**Table 18** Measurements of *Ichthyorachis newenhami* (in mm). N=10.

| | NM | x | Mn | Mx | CVw | CV |
|---|---|---|---|---|---|---|
| MBW | 45 | 0.70 | 0.55 | 0.87 | 5.52 | 8. |
| LBW | 23 | 0.57 | 0.50 | 0.70 | 8.15 | 11. |
| LBS | 27 | 1.40 | 1.05 | 1.75 | 8.46 | 11. |
| AD | 111 | 0.13 | 0.10 | 0.20 | 9.10 | 7. |
| AS | 113 | 0.36 | 0.22 | 0.45 | 12.46 | 14. |

DISCUSSION. Although only 10 colonies of *Ichthyorachis newenhami* were measured it was found that they showed very lit

morphological variation. Main stem width, lateral branch width, lateral branch spacing, and autozooecial apertural diameter all display low coefficients of variation, both within and between colonies. A slightly larger variation occurs in autozooecial apertural spacing. *Ichthyorachis newenhami* is a distinctive but uncommon fenestrate form found in the Carboniferous of the British Isles. It has previously been reported only from Counties Cork and Limerick (M'Coy 1844), Hook Head in County Wexford (Courceyan) (Dresser 1960), and Castleton in Derbyshire (Vine 1883, 1884a).

Examination of some of the type specimens of *Penniretepora triserialis* Owen, 1966 from the Upper Viséan of Treak Cliff, Castleton, Derbyshire (holotype: LL.2978; paratype: LL.2980) shows that autozooecia are arranged in three rows on mainstems and in two rows on lateral branches. This arrangement is characteristic of *Ichthyorachis*, and conceptually cannot be attributed to *Pennirepora*. The gross size of the specimens shows them to lie within the range exhibited by *I. newenhami*. The remaining type material of *P. triserialis* (paratypes: LL.2979, LL.2981-2983), also from the Upper Visean of Treak Cliff, Castleton, Derbyshire, has been examined and the 'third row of autozooecia' on mainstems are found to be the cores of abraided carinal nodes. These specimens belong to an indeterminate *Pennirepora* species and *P. triserialis* Owen, 1966 is herein regarded as a species inquirenda.

Lower Devonian species of *Ichthyorachis* are also known. *I. nereis* occurs in the Helderbergian of New York (Hall 1874), and *Ichtyorachis* [sic] sp. has been found in the Emsian of France (Rondeau 1890, Bigey 1973).

King (1849, 1850) referred *Ichthyorachis* to his genera *Acanthocladia* and *Thamniscus* owing to the similarities of the branching pattern with the former, and autozooecial arrangement with the latter. Comparison of the three taxa shows King's reasoning to be incorrect. *Ichthyorachis* is very distinct from the other two taxa. Branches in both *Acanthocladia* and *Thamniscus* are more robust and irregular than in *Ichthyorachis*, and distinct peristomial rims are developed around autozooecial apertures in *Thamniscus*.

*Ichthyorachis* does, however, resemble *Baculopora* Wyse Jackson 1988 in the development of 4 or more rows of autozooecia on branches. However, the two taxa are generically distinct in that *Ichthyorachis* bears regular lateral branches on both sides of the main stem and *Baculopora* does not.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Courceyan–Asbian).

DISTRIBUTION. British Isles.

Family **FENESTELLIDAE** King, 1850
Genus ***THAMNISCUS*** King, 1849

TYPE SPECIES. *Keratophytes dubius* Schlotheim, 1820 by original designation from the Permian of Germany.

***Thamniscus colei*** Wyse Jackson, 1988 Fig. 48

MATERIAL. BMNH PD8960-8982; TCD.29314-29323, TCD.34152, 42606b; NMI:F19531-F19540; BELUM K2154, K2157, K2166, K2223, K12118-K12127, Upper part of the Glencar Limestone, Viséan (Asbian), Carrick Lough, County Fermanagh. BMNH PD8959, 8983-8985; TCD.42543-42546, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. The zoarium is small and develops from a flared basal holdfast to an open basket 7mm wide. The heavily calcified holdfast is barren of apertures, whereas apertures open on the outer side of the basket. Branches are very robust (1.40 mm maximum width), circular in cross-section and bifurcate at irregular intervals at a high angle. Branches maintain a constant width along their length, and there is no increase in branch width prior to or following bifurcation. Branch surfaces are smooth. Autozooecial apertures are arranged in two to five sub-linear rows in an irregular pattern on the obverse branch surface. The outer peristomial rims of the lateral rows of apertures protrude slightly beyond normal branch margins giving them an undulatory appearance. Autozooecial apertures are circular, large and are surrounded by prominent thin peristomes. Autozooecial chambers are elongate, circular in cross-section, and narrow proximally.

DISCUSSION. A complete systematic description of *T. colei* is given in Wyse Jackson, 1988.

Suborder **PHYLLOPORININA** Lavrentjeva, 1979
Family **CHAINODICTYONIDAE** Nickles & Bassler, 1900
Genus ***RHOMBOCLADIA*** Rogers, 1900

TYPE SPECIES. *Rhombocladia delicatula* Rogers, 1900 by original designation from the Upper Carboniferous of Kansas, U.S.A.

REVISED DIAGNOSIS. Chainodictyonid with unilaminate, ramose zoarium, with dichotomous branches which are oval to elliptical in cross-section. Autozooecia are arranged in 4 to 12 longitudinal rows on obverse surfaces only. Superior hemisepta well developed; basal diaphragms rare. Autozooecial apertures oval. Reverse surface covered with thin semi-circular ridges.

STRATIGRAPHICAL RANGE. Lower Carboniferous–Lower Permian.

DISTRIBUTION. British Isles, Europe, North America, the CIS (former Soviet Union), China.

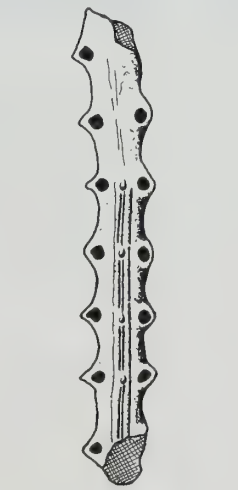


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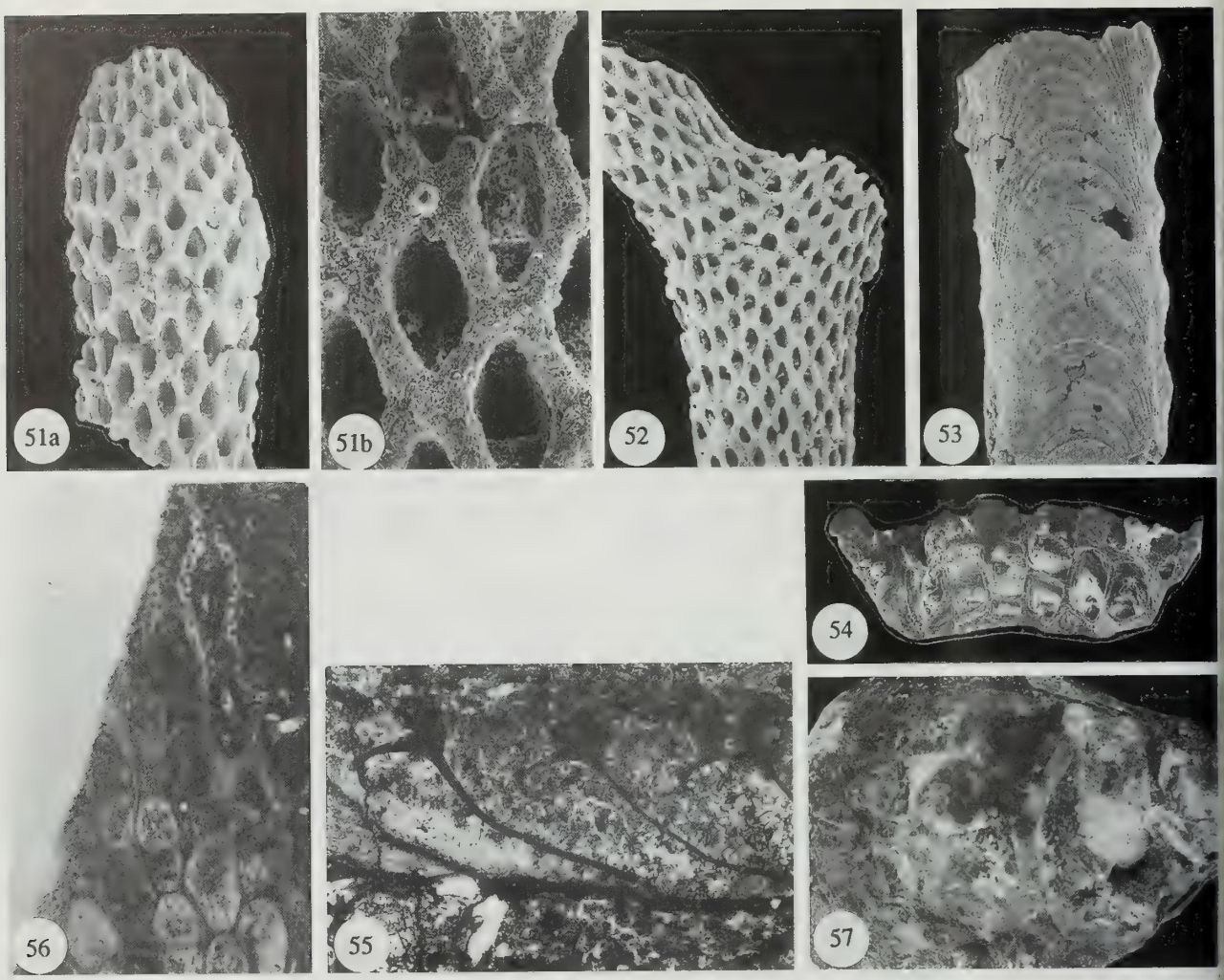
**Fig. 49** *Diploporaria marginalis* (Young & Young, 1875a). Line drawing of external features of BMNH PD9580; scale bar = 1 mm.

**Fig. 50** *Ichthyorachis newenhami* M'Coy, 1844. Line drawing of external features of BMNH PD9581; scale bar = 1 mm.




**Figs 51–57** *Rhombocladia dichotoma* (M'Coy, 1844) comb. nov.; **51–56,** Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **51,** BMNH PD9591; **51a,** obverse surface details of a growing tip; autozooecia are arranged in eight longitudinal and obliquely intersecting rows; autozooecial apertures are rhombic in shape, ×40; **51b,** detail of autozooecial apertures together with that of the hemiseptum developed from proximal walls; note the position of a single acanthostyle distal of autozooecia, ×150; **52,** BMNH PD9592, obverse surface of a branch with 11–12 rows of autozooecia, ×20; **53,** BMNH PD9593, reverse surface detail showing characteristic semi-circular pattern of basal laminae, ×40; **54,** BMNH PD9593, broken zoarial fragment showng typical cross-section shape of branches, ×80; **55,** BMNH PD9618, longitudinal section showing autozooecial chamber shape, thin chamber walls, and long hemisepta, ×50; **56,** BMNH PD9614, shallow tangential section showing longitudinal arrangement of autozooecia, with cross-cut hemisepta, and heterostyles developed on interapertural walls, ×40; **57,** NMI.F6030, **(lectotype)**, Carboniferous Limestone, Dinantian (Viséan); locality uncertain; Griffith Collection, reverse surface of branched zoarium showing characteristic semi-circular pattern of basal laminae, and longitudinal lines where autozooecial walls meet basal wall; figured by M'Coy, 1844, pl. 27, fig. 15 as *Vincularia dichotoma*; ×2.

***Rhombocladia dichotoma*** (M'Coy, 1844) comb. nov.
Figs 42c, 51–58

v 1844 *Vincularia dichotoma* M'Coy: 198, pl. 27, fig. 15.
*non* 1850 *Vincularia dichotoma* d'Orbigny, p. 195, pl. 682, figs 7–9.
1854b *Vincularia dichotoma* M'Coy; M'Coy: 104.
1857 *Vincularia dichotoma* M'Coy; Jukes: 454.
1862 *Vincularia dichotoma* M'Coy; Griffith: 198, 235.

LECTOTYPE. NMING:F7058, here designated; Black Lion, near Enniskillen, County Cavan (Viséan, Asbian); Griffith Collection.

PARALECTOTYPES. NMING:F6030, here designated; no locality given (?Viséan); Griffith Collection; figured M'Coy 1844, pl. 27, fig. 15. NMING:F7056-F7057, F7059-F7060; Black Lion, nea Enniskillen, County Cavan (Viséan, Asbian); Griffith Collectio NMING:F7061; Millicent, Clane, County Kildare (Viséan, Chadian Griffith Collection. NMING:F7486-F7489; Kildare, County Ki dare (Viséan); Griffith Collection. SMC:E5188; Howth, Coun Dublin (Courceyan/Chadian, Dinantian); Griffith Collectio SMC:E5189/a–b; Killymeal, Dungannon, County Tyrone (Viséa Brigantian); Griffith Collection. SMC:E5190; Kildare, County Ki dare (Viséan); Griffith Collection.

MATERIAL. BMNH D2564; ?Ireland (?Carboniferous); Shrubso Collection. BMNH PD9591-9620; TCD.34053-34064, 3415 34164, 34167, 42563a, b, 42565-42567, 42594, 42604c, 42606 42609; BELUM K2159, Upper part of the Glencar Limesto

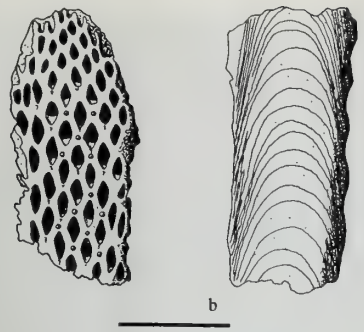



**Fig. 58** *Rhombocladia dichotoma* (M'Coy, 1844) comb. nov. Line drawing of external features; **a,** obverse surface (BMNH PD9591); **b,** reverse surface (BMNH PD9593); scale bar = 1 mm.

(Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42547-42549, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

M'COY'S ORIGINAL DIAGNOSIS. 'Dichotomous; obverse rounded, with about six equal, parallel, slender, longitudinal ridges, in the concave furrows, between which are five rows of oval, prominent cells, the marginal furrow on each side free of cells; reverse flat, with numerous, semicircular, scale-like wrinkles, and about six longitudinal striae.'

EMENDED DIAGNOSIS. *Rhombocladia* with a ramose zoarium of dichotomising branches oval to elliptical in cross-section. Seven to twelve longitudinal rows of autozooecial apertures open onto the obverse surface. A single superior hemiseptum is developed on the proximal side of apertures and basal diaphragms are rare. Interapertural areas smooth, or with small pustules.Autozooecial apertures oval to rhombic in shape; a single large acanthostyle occurs proximally at each autozooecial aperture. Reverse surface barren, with parallel semi-circular ridges along the length of branches.

DESCRIPTION. Zoaria are ramose with dichotomously dividing flattened branches. In cross-section branches are oval to elliptical in shape, and convex frontally. The largest fragment examined measures 30.4mm in length.

Autozooecial apertures open on the obverse surface only, and are arranged into 7 to 12 longitudinal rows. The number of rows along a branch is usually stable until a bifurcation point is reached, where the shape and size of apertures becomes variable and the regularity of their organization is lost. Uniformity returns distally beyond bifurcations. Narrow, barren marginal zones on the obverse surface are common in most zoaria. Autozooecial apertures are commonly oval to rhombic, rarely an acute hexagonal shape. Oval apertures are most common along branch margins, with rhombic shapes predominating towards the branch centre.

Interapertural walls are thin and smoothly rounded. They are smooth or bear faint pustules, and a single large acanthostyle, up to 0.18mm in length and 0.03–0.08mm in width, is situated proximally of each aperture. In most zoaria the large acanthostyles have been abraded down to the zoarial surface and are evident only as small areas of coarser skeleton.

The reverse surface, formed by the colony basal wall, is undulatory, very thin (0.1mm), and bears thin, parallel, semicircular lines along the entire length of branches (apparently marking former positions of the growing tips of branches). Where the basal wall is abraded a series of up to 10 longitudinal rows, representing the proximal portions of autozooecial chamber walls, is visible.

Autozooecial chambers originate on the basal wall and distally curve upwards at a low angle. At the junction of the endozone and exozone the chamber bends abruptly upwards. Here a prominent superior hemiseptum (average length 0.15mm) is developed, and is a little reflexed distally. Large acanthostyles originate at the base of the exozone. Endozonal walls are thin (0.01mm). Diaphragms are thin and are found only in the basal areas of the endozone.

**Table 19** Measurements of *Rhombocladia dichotoma* (in mm). N=18.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZW | 71 | 1.79 | 0.80 | 3.13 | 7.95 | 4.39 |
| ZT | 23 | 0.47 | 0.30 | 0.56 | 8.16 | 8.97 |
| AR | 41 | 10 | 7 | 12 | 6.66 | 8.60 |
| ZL2 | 134 | 4.89 | 4 | 7 | 7.26 | 8.19 |
| ZT1 | 97 | 3.87 | 3 | 6 | 10.72 | 8.89 |
| AD1 | 160 | 0.27 | 0.19 | 0.42 | 9.14 | 6.97 |
| AD2 | 160 | 0.12 | 0.08 | 0.18 | 11.73 | 6.64 |
| AS1 | 160 | 0.09 | 0.07 | 0.32 | 19.81 | 4.50 |
| AS2 | 160 | 0.07 | 0.04 | 0.13 | 14.13 | 4.63 |
| AW | 87 | 0.04 | 0.03 | 0.08 | 15.26 | 4.13 |
| AH | 21 | 0.12 | 0.02 | 0.18 | 17.29 | 0.65 |
| HL | 6 | 0.15 | 0.10 | 0.19 | 9.82 | 2.53 |
| ET | 9 | 0.33 | 0.30 | 0.38 | 6.01 | 15.79 |
| TE | 8 | 0.13 | 0.09 | 0.17 | 10.86 | 3.81 |
| AWT | 7 | 0.01 | 0.01 | 0.02 | 16.67 | 9.19 |

DISCUSSION. M'Coy (1844) described and figured *Vincularia dichotoma* from the Carboniferous of Ireland. On the basis of M'Coy's types and conspecific specimens from the Viséan of County Fermanagh, this species is here reassigned to the genus *Rhombocladia* Rogers, 1900. Of the eleven specimens examined by M'Coy and still in existence, none show the obverse surface. M'Coy must therefore have had additional specimens available which are presumed lost. The lateral margin of specimen NMING:F7058 is slightly worn and shows some detail of internal structure, enabling it to be compared to material from Carrick Lough, examined in the present study. All the material is conspecific and NMING:F7058 is here selected as the lectotype for the species *Rhombocladia dichotoma*.

In many cases early workers assigned cylindrical Bryozoa to the genus *Vincularia* which is in fact a cheilostome genus. 16 species of *Rhombocladia* have been previously described. Of these 13 occur in the Carboniferous and have been recorded from from the United States (McKinney 1972, Rogers 1900), the CIS (former Soviet Union) (Dunaeva 1961, Gorjunova 1988, Shulga-Nesterenko 1955), the Carnian Alps (Ceretti 1963, 1964), and China (Lu 1989). Three species have been recorded from the Permian: *R. aktashensis* from the CIS (former Soviet Union) (Lavrentjeva 1985) and *R. minor* and *R. spinulifera* from Western Australia (Crockford 1944).

Table 20 shows morphological measurements for all species of *Rhombocladia*. *R. dichotoma* differs significantly from all species except *R. delicatula* Rogers which has a similar zoarial thickness, and number of autozooecial rows. However, in *R. delicatula* prominent superior hemisepta are not present as they are in *R. dichotoma*.

*Rhombocladia dichotoma* displays the greatest zoarial width of any of the taxa (maximum observed value = 3.13 mm) and the largest number of autozooecial rows. Apertural diameters within the genus are relatively constant. This explains the large width of branches observed in *R. dichotoma*.

Zoarial thickness in all species is similar, with the exception of *R. aktashensis* whose branches are sub-circular in cross-section. The ratio of zoarial width to zoarial thickness in Carboniferous species is approximately 3:1, compared to 3:2 for the Permian species.

McKinney (1972: 60) postulated an erect growth habit for *Rhombocladia* on the basis of the occurrence of a species of *Hederella* encrusting the reverse surface. This interpretation is questionable,

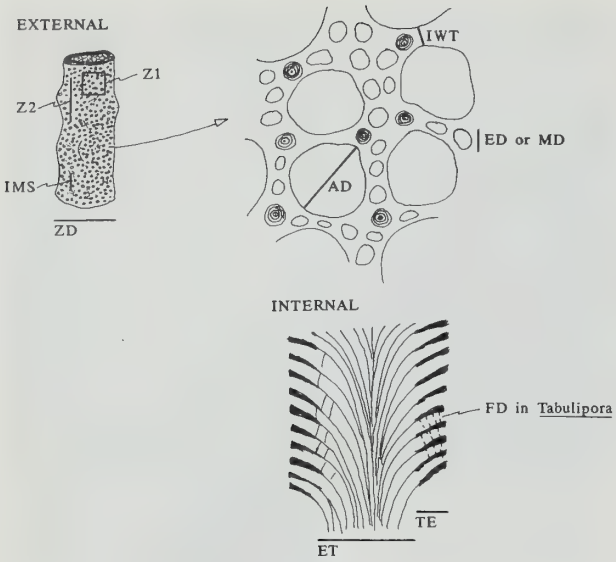



**Fig. 59** Measurements taken on trepostomes in this study: ZD = Zoarial diameter measured perpendicular to growth direction; IMS = Intermonticule spacing; AD = Autozooecia apertural diameter: maximum value seen in aperture; IWT = Interzooecial wall thickness; ED = Exilazooecia apertural diameter: maximum value seen in aperture; MD = Mesozooecial apertural diameter: maximum value seen in aperture; Z1 = Number of complete autozooecial apertures enclosed in 1mm$^2$; Z2 = Number of complete autozooecial apertures measured along a 2mm line; AR = Axial ratio: this measures the ratio of the exozone to the zoarial diameter [AR = 2(TE)/ZD; the method employed follows that of Boardman (1960: 21) rather than that of Cuffey (1967: 31) who multiplied the ratio by 100, which makes the obtained values unnecessarily large]; ET = Endozone thickness; TE = Exozone thickness; FD = Diameter of ring septum foramen.

and *Hederella* may have grown over a dead skeleton of *Rhombocladia* lying face downwards on the sea-bed. *Rhombocladia* may have hadan encrusting habit as some Carrick Lough specimens show that the zoarium grew around and engulfed some adjacent pinnate bryozoan colonies. The perpendicular attitude of these pinnate colonies, which grew erect, relative to colonies of *Rhombocladia*, suggests that *Rhombocladia* grew horizontally on or just above the sea-bed.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Tournasian [Courceyan]–Viséan [Brigantian]).

DISTRIBUTION. British Isles (Counties Cavan, Fermanagh, Kildare, and Tyrone, Ireland; Mill Gill, North Yorkshire, England).

Order **TREPOSTOMATA** Ulrich, 1882
Suborder **HALLOPOROIDEA** Astrova, 1965
Family **HETEROTRYPIDAE** Ulrich, 1890
Genus ***LEIOCLEMA*** Ulrich, 1882

TYPE SPECIES. *Callopora punctata* Hall, 1858, by original designation from the Lower Carboniferous of Iowa, U.S.A.

### *Leioclema indentata* sp.nov. Figs 60–62

HOLOTYPE. BMNH PD9621, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.

PARATYPES. BMNH PD9564, 9622-9626; TCD.34065-34066, 34123, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42550, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh. TCD.28152, Base of reef, Lower Carboniferous (Viséan, Asbian), Shanvaus Cross, County Leitrim, G.D. Sevastopulo Collection.

DERIVATION OF TRIVIAL NAME. From the indentation of the autozooecial apertures by acanthostyles.

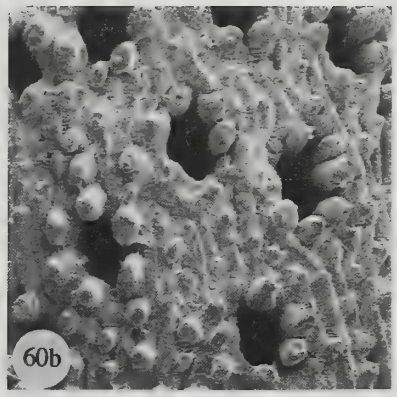
DIAGNOSIS. *Leioclema* forming ramose erect cylindrical, irregularly dichotomising zoaria. Zooecial walls considerably thickened in exozone. Diaphragms present at zooecial bend. Mesozooecia common between chambers in exozone, closed to the surface. Autozooecial apertures indented by several large acanthostyles.

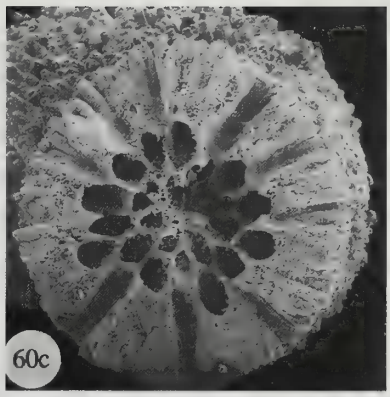
DESCRIPTION. Zoaria are robust, composed of straight, cylindrical branches 1.15 to 2.13 mm in diameter. Branches are circular in cross-section and bifurcate at irregular intervals. There is a slight increase in branch diameter prior to division; subsequent branches are slightly narrower. The largest fragment examined measures 24.5 mm long.

**Table 20** Quantitative measurements for all described species of *Rhombocladia* (in mm).

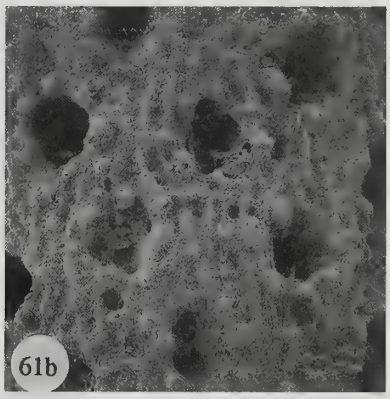
| | ZW | ZT | AR | AD1 | AD2 | AS | HL |
|---|---|---|---|---|---|---|---|
| *R. dichotoma* (M'Coy,1844) | 1.79 | 0.47 | 7–12 | 0.27 | 0.12 | 0.07–0.14 | 0.15 |
| *R. aktashensis* Laurentjeva, 1985 | 1.50–1.80 | 1.00–1.1 | 6–8 | 0.22–0.24 | 0.12 | 0.10–0.15 | 0.03 |
| *R. borissiaki* Shulga-Nest., 1955 | 1.00–1.35 | 0.45–0.50 | 7–8 | 0.26–0.34 | 0.12–0.14 | – | 0.03–0.0 |
| *R. carnica* Ceretti,1964 | 0.60 | – | – | 0.30 | 0.13 | 0.09–0.10 | – |
| *R. coronata* Shulga-Nest., 1955 | 1.10 | 0.45 | 6–8 | 0.19–0.20 | 0.08–0.15 | 0.20–0.27 | – |
| *R. delicatula* Rogers, 1900 | 1.50 | 0.52 | 10 | 0.26 | 0.15 | 0.10 | – |
| *R. johnseni* Ceretti, 1964 | 1.07 | 0.50 | 7 | 0.20 | 0.21 | 0.09 | – |
| *R. kasimovensis* Shulga-N., 1955 | 0.80–1.20 | 0.45–0.70 | 5–7 | 0.15–0.22 | 0.08–0.12 | – | – |
| *R. minor* Crockford, 1944 | 0.46–0.57 | – | 2–3 | 0.24–0.29 | 0.10–0.15 | – | – |
| *R. multispinosa* McKinney, 1972 | 1.4 | <1.00 | 9 | 0.30–0.42 | 0.12–0.19 | – | – |
| *R. ninae* Shulga-Nest., 1955 | 1.70–2.30 | 0.70–0.80 | 8–9 | 0.20–0.22 | 0.10–0.12 | 0.22–0.28 | 0.02 |
| *R. orientalis* Lu, 1989 | – | 0.30–0.50 | – | 0.22 | 0.16–0.18 | – | – |
| *R. punctata* Dunaeva, 1961 | 1.00–1.08 | 0.48 | – | 0.24–0.27 | 0.12 | – | – |
| *R. ramosa* Gorjunova, 1988 | 1.10–1.32 | 0.86–0.88 | 6–7 | 0.18–0.22 | – | – | – |
| *R. septata* Shulga-Nesterenko, 1955 | 1.25 | 0.45–0.52 | 7 | 0.27–0.32 | 0.12–0.14 | 0.15–0.20 | 0.0 |
| *R. spinulifera* Crockford, 1944 | 0.70–0.95 | – | 4–6 | 0.19–0.24 | 0.16 | – | – |
| *R. tenuata* Shulga-Nesterenko, 1955 | 0.80 | 0.50 | 7 | 0.18–0.20 | 0.10–0.12 | – | – |

Data from original sources.






**Figs 60, 61** *Leioclema indentata* sp. nov.; **60,** Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; BMNH PD9621 **(holotype)**; **60a**, ramose colony with circular autozooecial apertures arranged in crude longitudinal rows, surrounded by large acanthostyles, with ridged interapertural areas, ×15; **60b,** detail of 60a, showing oval-shaped autozooecial apertures surrounded by six to eight large acanthostyles; smaller acanthostyles are developed in interapertural areas, ×85; **60c,** cross-sectional view showing central axial region of thin walled autozooecial chambers and very thick exozone region, ×30; **61,** base of reef, Lower Carboniferous (Viséan, Asbian), Shanvaus Cross, County Leitrim, TCD.28152; **61a**, ramose colony., ×20; **61b,** detail of 61a showing small circular mesozooecial apertures between autozooecial apertures, ×100.

Autozooecia are developed throughout the zoarium. The exact shape of the zooecial chambers is unknown. It appears that the chambers diverge from the centre of the branch at a low angle of 25° to 30°. Zooecia bend through 50° at the endozone/exozone boundary so that vestibules are orientated perpendicular to the zoarial surface. Chamber walls are thin (0.01–0.02 mm) in the endozone and thicken rapidly at the exozone which reaches a maximum thickness of 1.10 mm. Thin diaphragms are common at the base of the vestibule. In cross-section chambers are circular, pentagonal or polygonal in shape.

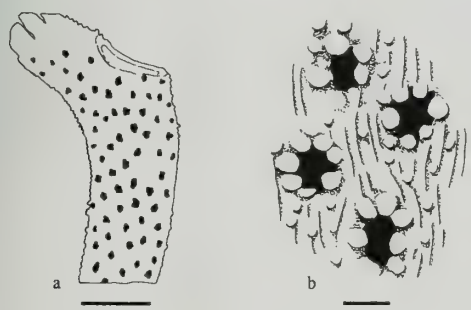



**Fig. 62** *Leioclema indentata* sp. nov. Line drawing of external features of BMNH PD9621; **a,** colony form, scale bar = 1 mm; **b,** Detail of surface features, scale bar = 0.1 mm.

Mesozooecia are common in the exozone, where they are disposed in three to five irregular rows between autozooecial chambers, but are not present in the endozone. They are circular, polygonal or irregular in shape, 0.03 to 0.11 mm in diameter, thin walled, hollow, and closed to the surface. No internal diaphragms were observed, perhaps due to the nature of the preservation.

Autozooecial apertures are oval in shape, moderately large 0.12 to 0.20 mm in diameter, and fairly regularly spaced one to two diameters apart. They are arranged in 16 to 20 poorly defined longitudinal rows. Each aperture is surrounded by six to seven large acanthostyles (0.05 to 0.08 mm in width and up to 0.1 mm in length), which indent the aperture margin.

Smaller ramdomly orientated acanthostyles, and thin wavy longitudinal grooves are found in interapertural areas which are slightly

**Table 21** Measurements of *Leioclema indentata* (in mm). N=6.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 61 | 1.66 | 1.15 | 2.13 | 6.92 | 7.38 |
| AD | 60 | 0.15 | 0.12 | 0.20 | 9.40 | 9.88 |
| IWT | 60 | 0.18 | 0.06 | 0.26 | 17.33 | 9.22 |
| Z1 | 60 | 6.23 | 4 | 8 | 10.48 | 11.11 |
| Z2 | 60 | 3.60 | 3 | 5 | 13.48 | 9.11 |
| ET | 9 | 0.84 | 0.68 | 1.10 | 2.69 | 5.17 |
| TE | 18 | 0.38 | 0.28 | 0.51 | 8.89 | 6.68 |

**Table 22** Quantitative comparision of *Leioclema indentata* with other Carboniferous *Leioclema* species (dimensions in mm).

| | ZD | AD | IWT | Z2 | ET | TE |
|---|---|---|---|---|---|---|
| *L. indentata* sp. nov. | 1.15–2.18 | 0.12–0.20 | 0.06–0.26 | 4–8 | 0.68–1.10 | 0.28–0.51 |
| *L. porosum* Crockford, 1947 | 20 | 0.2–0.25 | 0.08 | – | – | – |
| *L. shumaradi* Girty, 1908 | 3.5 | 0.15–0.20 | 0.20 | – | – | – |
| *L. punctatum* (Hall, 1858) | 2.00–5.00 | 0.15–0.20 | – | 5–6 | – | – |
| *L. pushmatahensis* Harlton, 1933 | 0.73–1.02 | – | – | – | – | |
| *L. avonense* Lee, 1912 | 22.00 | – | – | 6 | – | – |
| ?*L. hirsutum* Moore, 1929 | 1.00–1.40 | 0.16–0.20 | 0.1 | – | 0.9 | 0.40–0.45 |
| *L. tubulosa* Nekhoroshev, 1956 | 3.00–5.00 | 0.13–0.17 | – | 5.5–6.5 | – | – |
| *L. bifoliata* Nikiforova, 1927 | 4.0 | 0.20–0.25 | 0.1 | – | 1.2 | 0.8 |
| ?*L. kobayashii* Sakagami, 1962 | 2.60–3.60 | 0.21–0.29 | 0.32–0.40 | – | – | – |
| ?*L. uzuraense* Sakagami, 1964 | – | 0.16–0.22 | – | 10 | – | – |
| *L. cassis* Trizna, 1958 | 1.80 | 0.18–0.20 | – | 10 | – | – |
| *L. echinata* Trizna, 1958 | 1.60 | 0.16–0.18 | – | 7–10 | – | – |
| *L. podunskense* Trizna, 1958 | 2.20–3.20 | 0.15–0.18 | – | 5–7 | – | – |
| *L. rojkiensis* Trizna, 1958 | 2.00 | 0.20–0.22 | – | 6–7 | – | – |
| *L. semetra* Trizna, 1958 | 2.75–3.00 | 0.14–0.16 | – | 11–12 | – | – |
| *L. textila* Trizna, 1958 | 0.80–0.90 | 0.10–0.16 | – | 6 | – | – |
| *L. clara* Trizna, 1962 | 3.30 | 0.16–0.20 | – | 8–9 | – | – |
| *L. gracillimum* Ulrich, 1888b | 1.00–1.50 | 0.10–0.15 | – | 8–9 | – | – |
| *L.araneum* Ulrich, 1890 | Adnate 1.00 | 0.2 | – | 9–10 | – | – |
| *L.foliatum* Ulrich, 1890 | Adnate 1.00–1.50 | 0.2 | – | 6 | – | – |
| *L. subglobosum* Ulrich, 1890 | – | 0.15–0.20 | – | 8–9 | – | – |
| *L. washsmuthi* Ulrich, 1890 | Adnate <1.00 | 0.2 | – | 6 | – | – |

Data from original sources.

elevated above the autozooecial apertures. Monticules are not developed.

DISCUSSION. *Leioclema indentata* is very rare in the Viséan of County Fermanagh. Only ten zoarial fragments were found; all of these are silicified and consequently internal structures are not well known. However, some fine skeletal features such as autozooecial diaphragms are preserved, and are seen in broken fragments.

*L. indentata* can easily be recognised by the indentation of the autozooecial apertures by six to seven large acanthostyles, and from surface ornamentation. Coefficients of variation for measured parameters are all low, including that for interapertural wall thickness (IWT).

25 other *Leioclema* species have been described from the Carboniferous (McKinney 1973, Astrova 1978, and herein), of which only *L. avonense* Lee, 1912, from the Avon area, and *Leioclema* sp. from North Wales (Bancroft, Somerville & Strank, 1988), occur in the British Isles. All are compared with *L. indentata* in Table 22 above. *L. avonense* is unusual in that the zoarium is very thick, exozone walls are not thickened, and that mesozooecia are few. Thus, its taxonomic position is debateable, and may only be resolved by examining Lee's original material.

*L. indentata* has a gross morphology similar to the North American species *L. gracillimum* Ulrich, 1888b. However, apertural spacing and acanthostyle diameter are considerably less in the latter.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Viséan, Asbian).

DISTRIBUTION. Counties Fermanagh and Leitrim, Ireland.

## Suborder **AMPLEXOPORINA** Astrova, 1965
## Family **DYSCRITELLIDAE** Dunaeva and Morozova, 1967
## Genus ***DYSCRITELLA*** Girty, 1911

TYPE SPECIES. *Dyscritella robusta* Girty, 1911, by original designation from the Lower Carboniferous of Arkansas, U.S.A.

### ***Dyscritella miliaria*** (Nicholson, 1881) Figs 63–66

v1881 *Monticulipora tumida* var. *miliaria* Nicholson: 123, pl.3, fig.2.
1884c *Monticulipora tumida* var. *miliaria* Nicholson; Vine: 101.
1912 *Dyscritella miliaria* (Nicholson); Lee: 178, pl.16, figs 9,10.
1950 *Dyscritella miliaria* (Nicholson); Termier & Termier, p.15, pl.55, figs 4–6, 9, pl.60, fig.7, pl.65, figs 7–9.
1987 *Dyscritella miliaria* (Nicholson); Bancroft: 196.

LECTOTYPE. Herein designated AUGD 10135a, Carboniferous shales; Redesdale, Northumberland, England; Nicholson Collection.

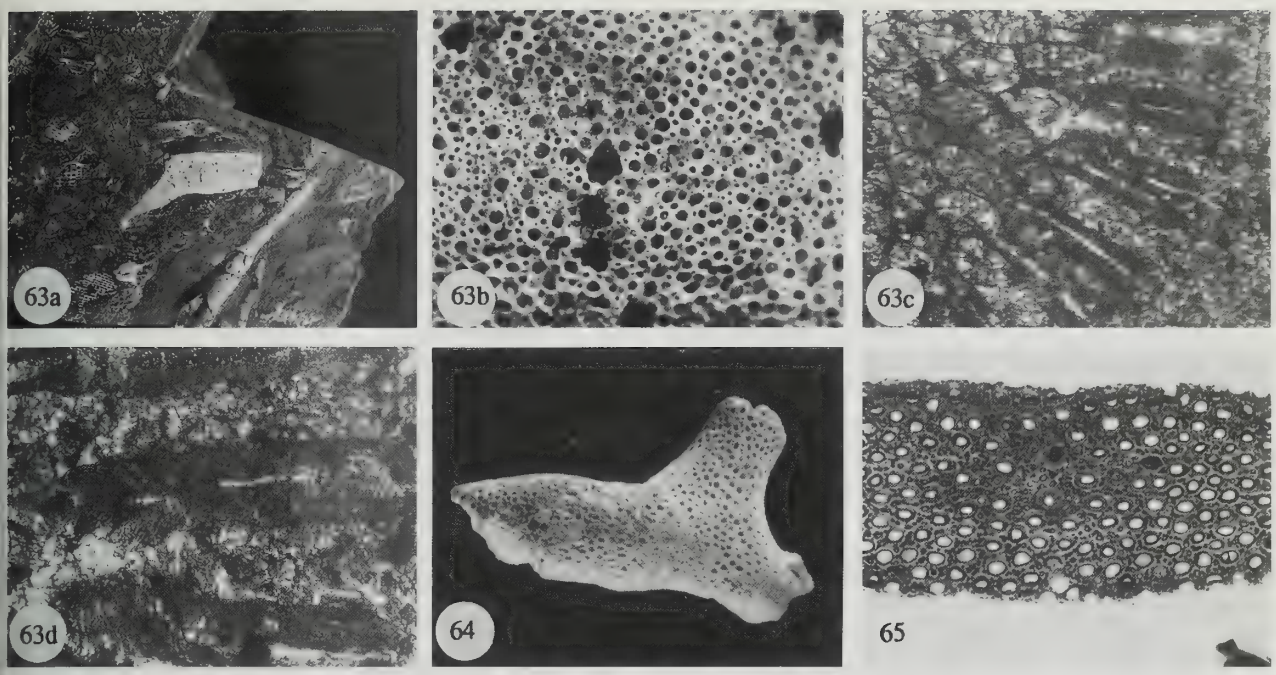
PARALECTOTYPES. Herein designated AUGD 10135b (2 specimens in cavity slide); Carboniferous shales; Redesdale, Northumberland, England; Nicholson Collection. RSM 1967.66.384, RSM 1967.66.387; Carboniferous shales; Redesdale, Northumberland, England; Nicholson Collection.

MATERIAL. BELUM K3442, K3608 Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DIAGNOSIS. *Dyscritella* with robust dendroid zoarium and irregularly dichotomising branches. Autozooecia are developed throughout the zoarium. Zooecial walls are thin in the endozone but are thick and of constant width in the exozone. Basal diaphragms are rare and indistinct. Autozooecial apertures are circular and of moderate size. Interapertural areas are of variable width, and exilazooecia are abundant. Maculae are quite common. Prominent, large acanthostyles occur at interzooecial intersections interspersed with smaller acanthostyles between.

DESCRIPTION. The dendroid zoarium is robust, the longest fragment examined attaining a length of 30.6mm. Bifurcation is rare but where it occurs no increase in branch width accompanies it.

Autozooecia originate in the endozone by interzooecial budding. From the endozone they diverge at a low angle, but in the exozone they turn through 80° to lie perpendicular to the zoarial surface. In the endozone zooecial walls are thin and undulatory. Walls thicken




**Figs 63–65** *Dyscritella miliaria* (Nicholson, 1881); **63,** Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh; BELUM K3442; **63a,** large zoarial fragments showing ramose growth-form and large circular autozooecial apertures surrounded by irregularly-placed exilazooecia, ×1; **63b**, detail of 63a, ×15; **63c,** cross-section showing autozooecial chambers with thickened exozonal walls, ×50; **63d,** detail of 63c, showing exilazooecium developed in exozone between adjacent autozooecial apertures, ×120; **64–65,** Carboniferous shales (probably Redesdale Ironstone Shale (Asbian), Lower Limestone Group), Redesdale, Northumberland; **64,** AUGD.10135a **(lectotype)**, ramose branching zoarial fragment with crowded arrangement of autozooecial apertures surrounded by much smaller circular or irregularly-shaped exilazooecial apertures, ×5; **65,** GSM 1967.66.384 (paralectotype), tangential section showing oval autozooecial apertures surrounded by numerous exilazooecia, ×15.

rapidly at the endozone/exozone boundary, and wall thickness remains constant (mean thickness 0.07mm) throughout most of the exozone. Thin basal diaphragms are infrequently developed in the endozone, whereas very thin diaphragms are occasionally developed in the exozone.

Autozooecial apertures are of moderate size, circular in shape, and are closely packed, approximately their own diameter apart.

Interapertural areas are irregular in width. Exilazooecia are very abundant between autozooecia and vary greatly in shape and size. They are usually circular to oval, but in interapertural angles small pentagonal forms occur (0.02–0.1mm in diameter). Frequently, one or two exilazooecia are located between autozooecia. Exilazooecia originate within the exozone where they form short, narrow tubes. Maculae, 0.4mm in diameter, occur occasionally and comprise clusters of exilazooecia.

Acanthostyles are abundant in interapertural walls. Relatively large acanthostyles (mean diameter 0.03mm) persist at interapertural angles around autozooecia while smaller acanthostyles (mean diameter 0.01mm) are developed in a line on interapertural walls between both autozooecia and exilazooecia.

**Table 23** Measurements of *Dyscritella miliaria* (in mm). N=5.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ED | 19 | 4.59 | 3.17 | 6.15 | 9.65 | 5.06 |
| E1 | 21 | 16.06 | 9 | 22 | 28.53 | 4.51 |
| E2 | 25 | 8.35 | 7 | 10 | 10.16 | 147.80 |
| AD | 30 | 0.12 | 0.09 | 0.22 | 12.08 | 5.34 |
| AWT | 30 | 0.08 | 0.03 | 0.28 | 38.77 | 2.30 |
| ED | 30 | 0.04 | 0.02 | 0.10 | 31.90 | 4.04 |
| ET | 9 | 2.64 | 1.91 | 3.52 | 13.47 | 5.50 |
| TE | 18 | 0.97 | 0.57 | 1.38 | 8.00 | 1.24 |
| AR | 9 | 0.57 | 0.50 | 0.70 | 6.43 | 12.96 |

DISCUSSION. This is the first reported occurrence of the trepostome *Dyscritella miliaria* from the Carboniferous of Ireland. The abundance of exilazooecia ('interstitial tubuli' of Nicholson, 1881) makes the taxon very distinctive. It was first described, as *Monticulipora tumida* var. *miliaria*, from the Lower Carboniferous of England (Nicholson 1881). Subsequent specimens from the Midland Valley of Scotland were discovered in the Young Collection at the Hunterian Museum (Bancroft 1984). *D. miliaria* also occurs at Llangollen, North Wales, in strata of Asbian age (A.J. Bancroft, *pers. comm.*, April 1988).

*Dyscritella miliaria* is rare in the Lower Carboniferous of the

**Fig. 66** *Dyscritella miliaria* (Nicholson, 1881). Line drawing of external features of BELUM K3442; scale bar = 0.1 mm.

British Isles. In the large bryozoan sample examined in this study only 4 specimens were found.

In his original description Nicholson failed to notice basal diaphragms in the endozone. Lee (1912) redescribed the earlier material in which he found ill-defined 'tabulae' (basal diaphragms). Consequently, he correctly placed the specimens in the genus *Dyscritella* and elevated *miliaria* from variety to specific rank.

Coefficient of variation values in Table 23 illustrate a number of features. Zoarial width (ZW) and autozooecial aperture diameter (AD) do not vary greatly either within or between colonies. The within-colony ranges of exilazooecial diameter (ED), autozooecial spacing (AS), and the number of autozooecia in an area of 1mm (Z1) are all large. However, between-colony CVs for these parameters are small because all colonies are of a similar size. There is little within-colony variation, but large between-colony variation in the number of autozooecia in a 2mm line (Z2). This large CV value may be a sampling error arising from the small sample size.

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian–?Brigantian).

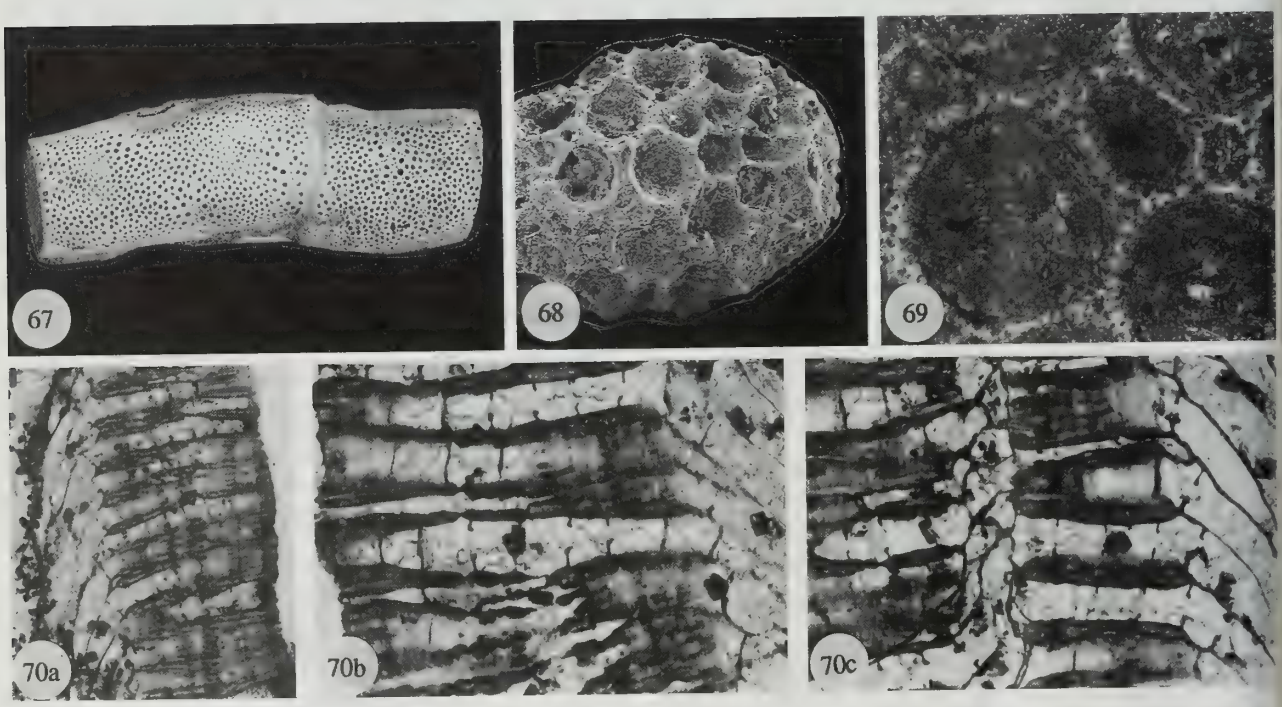
DISTRIBUTION. Ireland, northern England, North Wales, Midland Valley of Scotland, Morocco.

Family **STENOPORIDAE** Waagen & Wentzel, 1886
Genus ***TABULIPORA*** Young, 1883a

TYPE SPECIES. *Cellepora urii* Fleming, 1828 by monotypy from the Lower Carboniferous of East Kilbride, Scotland.

***Tabulipora urii*** (Fleming, 1828) Figs 67–70, 71a

| | |
|---|---|
| 1828 | *Cellepora urii* Fleming: 532. |
| v1883a | *Tabulipora urii* (Fleming); Young: 154. |
| v1883b | *Tabulipora urii* Young; Young: 264. |
| v1883 | *Tabulipora urii* Young [sic]; Nicholson: 295. |
| 1884b | *Tabulipora urii* Young [sic]; Vine: 380, pl. 20, figs 3a–b, 4. |
| 1912 | *Tabulipora urei* Young [sic]; Lee: 150. |
| 1912 | *Tabulipora scotica* Lee: 162, pl.14, figs 4a–d, pl. 15, figs 12, 13, 17, 18. |
| 1935 | *Tabulipora scotica* Lee; Anderson & Lamont: 216, fig. 6.13. |
| 1953 | *Tabulipora scotica* Lee; Bassler: G105, fig. 70 – 1a, 1b. |
| 1961 | *Tabulipora scotica* Lee; Wilson: 91. |
| 1969 | *Tabulipora scotica* Lee; Owen: 262, pl. 22, figs d–e. |
| 1970 | *Tabulipora urii* (Fleming); Gautier: 19, pl. 7, fig. 1; pl. 8, figs 1–2. |
| 1973 | *Tabulipora scotica?* Lee; Owen: 302. |
| 1977 | *Tabulipora urii* (Fleming); McKinney: 313, pl. 1, fig. 3. |
| *non* v 1986 | *Tabulipora scotica* Lee; Kora & Jux: 91, figs 3, g1–4. |
| 1987 | *Tabulipora urii* (Fleming); Bancroft: 196. |




**Figs 67–70** *Tabulipora urii* (Fleming, 1828); Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh; **67,** BELUM K15200, ramose colony fragment; autozooecia with circular to oval shaped apertures arranged over the whole surface, except on monticules; mesozooecia are developed between autozooecia, ×3; **68,** BMNH PD9638, small encrusting colony on ?echinoid spine, consisting of one layer of autozooecia with circular apertures with polygonal-shaped mesozooecia situated between, ×40; **69,** BMNH PD9472, shallow tangential section showing autozooecial and mesozooecial apertures, and interapertural walls with large acanthostyles at junctions and smaller stylets in between, ×35; **70,** BELUM K15207; **70a**, longitudinal section through thin-walled endozonal area and thickened exozone region; the initial portions of autozooecial chambers lie at a high angle to the zoarial surface, but bend at the exozone and become nearly perpendicular to it, ×12; **70b,** longitudinal section showing exozone and autozooecial chambers; ring septae develop at the top of the endozone with eight per autozooecium; septal necks are inflated and deflected interiorly, ×20; **70c,** longitudinal section showing exozone and autozooecial chambers, and zone of regeneration where the endozone is characteristically thin, ×20.

1988 *Tabulipora urii* (Fleming); Yang, Hu & Xia: 69, pl. 22, figs 5–8.

MATERIAL. BM(NH) PD9472, 9638-9642, 9704; TCD.34079, 42593b, 42604b, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; BELUM K15200-15208, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria are erect, ramose expansions of bifurcating cylindrical branches reaching 8.20mm in diameter.

Autozooecial chambers are budded interzooecially from the branch centres. Chambers diverge from the centre of branches at a low but constant angle of 30° in the endozone. They bend abruptly at the exozone; vestibules are orientated at angles of between 70° and 80° to the zoarial surface. Autozooecial chambers are ten to twelve times longer than wide. Chamber walls are very thin (0.01mm) in the endozone, but thicken considerably (to 0.05mm) in the exozone, where in some specimens as many as five monilae may occur. They are pear to oval-shaped thickenings of the chamber wall, and may be separated by lengths of thin chamber wall. Skeletal laminae within the wall are deflected away from the zoarial surface from a central dark zone at autozooecial boundaries. In cross section and deep tangential section chambers are polygonal in shape. Ring septa are developed in autozooecial chambers towards the top of the endozone and throughout the exozone. A solitary or pair of thin, widely spaced endozonal ring septa contrast with up to seven thicker and more closely spaced ring septae developed in the exozone. Foramen are circular or oval in shape and are placed either centrally or slightly laterally. The central walls of ring septa constitute a thickened ring that is bent posteriorly. Autozooecial apertures are large, circular to oval in shape, and closely spaced at less than one diameter apart. They are irregularly arranged over the zoarial surface. They are poorly developed on monticules where they are marginally larger. The long axes of oval shaped apertures radiate out from monticules and maculae. Interapertural walls are thin. Exilazooecia are very common, and are disposed in one or two rows between autozooecial apertures, or in radiating maculate clusters of up to forty individuals. They are small, thin walled, and circular to polygonal in shape.

Stylets are common and structurally variable, and developed on the thin interapertural walls. Large acanthostyles, 0.04mm in diameter, are found at interapertural junctions. These have a distinctive dark grey core developed from the base of the exozone. Smaller heterostyles (0.01–0.02mm in diameter) are found in one or two rows between acanthostyles. They arise from within the exozone.

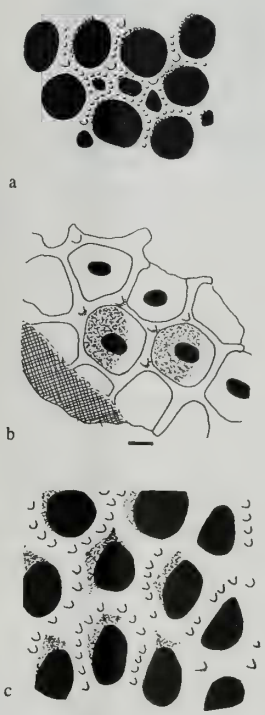



**Fig. 71** Line drawing of external features of the *Tabulipora* species described in this study. **a**, *Tabulipora urii* (Fleming, 1828) (BELUM K15200); **b**, *Tabulipora howsii* (Nicholson, 1881) (BMNH PD9644); **c**, *Tabulipora minima* Lee, 1912 (BMNH PD9650); scale bar = 0.1 mm.

**Table 24** Measurements of *Tabulipora urii* (in mm). N=8.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 69 | 5.59 | 3.79 | 8.20 | 3.84 | 5.34 |
| Z1 | 80 | 10 | 7 | 14 | 11.99 | 10.48 |
| Z2 | 80 | 5.85 | 4 | 7 | 10.73 | 10.48 |
| AD | 80 | 0.19 | 0.11 | 0.29 | 15.55 | 9.71 |
| IWT | 80 | 0.11 | 0.06 | 0.17 | 18.08 | 13.33 |
| ED | 80 | 0.07 | 0.05 | 0.14 | 22.98 | 6.95 |
| ET | 17 | 1.77 | 0.70 | 2.76 | 5.99 | 2.17 |
| TE | 33 | 0.97 | 0.47 | 1.98 | 12.51 | 2.17 |
| IMS | 8 | 4.72 | 4.10 | 5.94 | 17.47 | 11.32 |

DISCUSSION. *Tabulipora urii* was first described and figured by Ure (1793) as *Millepore* from the Carboniferous of Kilbride, West Scotland. Subsequently, Fleming (1828) cited Ure's material as the type species of his species *Cellepora urii*. This species was later described by Young (1883a) who noted ring septa in the autozooecial chambers and on the strength of this erected the subgenus *Tabulipora*. *Cellepora urii* is the type species of *Tabulipora* by monotypy.

Lee (1912) revised the British Trepostomata. He examined Young's material and erected a new species, *Tabulipora scotica*, designating it as the type species of *Tabulipora*. He demoted *T. urii* (misspelt '*urei*') because he felt that Young had not really proposed it as a new specific name, and because his material contained several species, none of which had been figured. Gautier (1970) stated that *T. urii* is the type species by monotypy, and thus *T. scotica* is invalid. *T. scotica* is regarded as a junior synonym of *T. urii* (Bancroft 1984: 372).

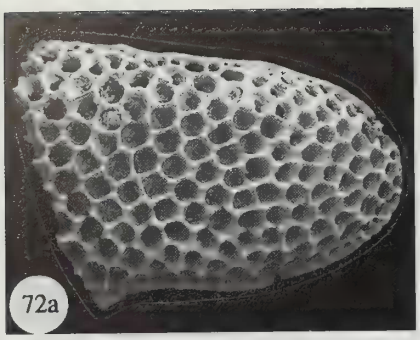
The figured specimens of *T. scotica* described from Egypt (Kora & Jux, 1986) have been examined. Up to nine hemiphragmas are developed in chambers indicating that the specimens are referable to the genus *Stenophragmidium*.

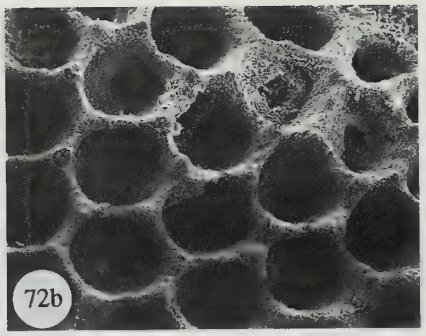
STRATIGRAPHICAL RANGE. Lower Carboniferous (Tournaisian–Brigantian).

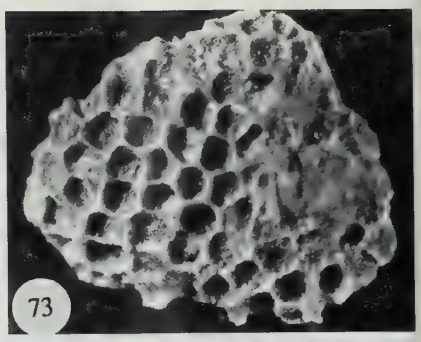
DISTRIBUTION. County Fermanagh, Midland Valley of Scotland, ?China.

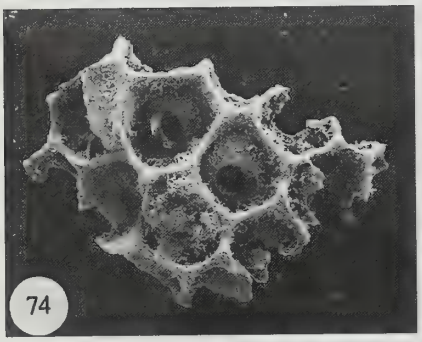
### *Tabulipora howsii* (Nicholson, 1881) Figs 71b, 72–78

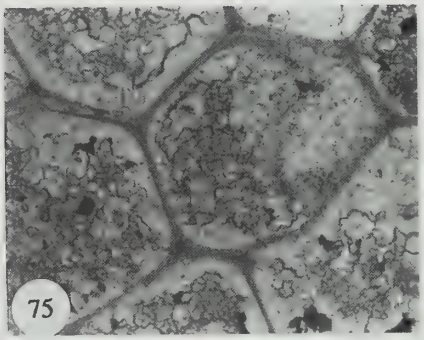
v1881 *Stenopora howsii* Nicholson: 83, fig. 12.
v1883 *Stenopora howsii* Nicholson; Nicholson: 285, pl. 10, figs 1–10, text-figs 1a–c.
1886 *Stenopora howsii* Nicholson; Nicholson & Etheridge jun.: 177.
v1889 *Stenopora howsii* Nicholson; Nicholson & Lydekker: 356, fig. 232.
1891 *Stenopora howsii* Nicholson; Etheridge jun.: 48.
1912 *Tabulipora howsei* [sic] (Nicholson); Lee: 166, pl. 14, figs 9a–c; pl.15, figs 22–24.

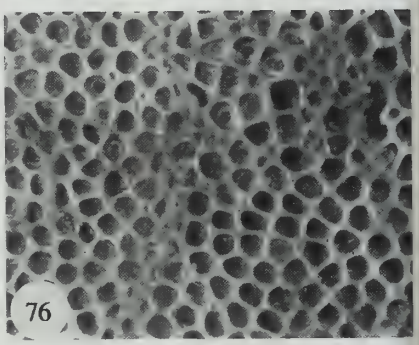


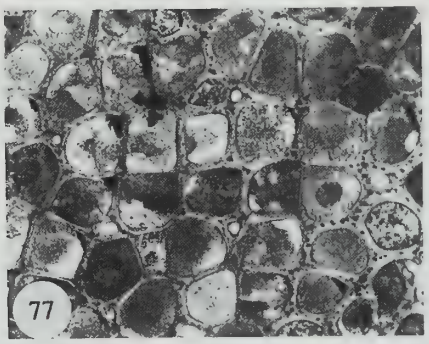



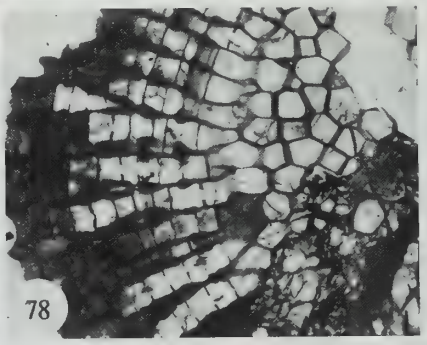




**Figs 72–78** *Tabulipora howsii* (Nicholson, 1881); **72–75,** Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **72,** BMNH PD9643; **72a,** adnate zoarium showing regular arrangement of autozooecia with circular apertures, ×12; **72b**, detail of 72a, showing circular autozooecial apertures with ring septa and circular-oval foramen, and acanthostyles positioned on interapertural wall junctions, ×40; **73,** BMNH PD9645, adnate zoarium, ×20; **74,** BMNH PD9644, as 72a, including ring septa with circular-oval foramen, ×50; **75,** BMNH PD9561, longitudinal section showing thin autozooecial chamber walls with acanthostyles developed on interapertural wall junctions, ×100; **76–78,** probably Redesdale Ironstone shale (Asbian), Lower Limestone Group, Redesdale, Northumberland; **76,** AUGD.10134a (paralectotype), detail of zoarial surface, ×20; **77,** AUGD.10134b **(lectotype)**, shallow tangential section showing arrangement of polygonal autozooecial chambers, centrally placed circular to oval foramen in some autozooecial chambers, rare exilazooecia, and stylelets of two sizes on thin interapertural walls – acanthostyles at wall junctions and heterostyles in between, ×40; **78,** AUGD.10134c (paralectotype), transverse section through branch showing inner endozone with thin-walled polygonal autozooecial chambers, and outer exozone with moniliform walls and 7–8 ring septa developed per chamber, ×20.

1913 *Tabulipora howsei* [sic] (Nicholson); Wright *et al.*: 72.
1925 *Tabulipora howsei* [sic] (Nicholson) var. nov. Smyth: 150.
1987 *Tabulipora howsii* (Nicholson); Bancroft: 196.
1991 *Tabulipora* cf. *howseii* [sic] (Nicholson); Billing: 41.

LECTOTYPE. Herein designated AUGD 10134b (fig. 12a of Nicholson 1881)

PARALECTOTYPES. Herein designated AUGD 10134, 10134a, and 10134c (fig. 12b of Nicholson 1881). AUGD 10132 and 10141 may be part of the original Nicholson material and so may also be paralectotypes (Benton & Trewin 1978, Benton 1979).

MATERIAL. BMNH PD9561, 9643-9649, 9653, 9722-9729; TCD.34080-34087, 34121, 34158, 34164, 42564, ; BELUM K2177, K3234, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42551-42554, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Only small encrusting zoaria were examined; no solid branches were recovered.

Adnate zoaria are thin, up to 1.30mm thick, and form small circular expansions up to 6.2mm in diameter. They encrust fenestrate bryozoans, and crinoidal material. Sheets are only one autozooecial chamber high; young autozooecia do not encrust older autozooecia (as in *Fistulipora incrustans*).

Autozooecia are budded from a thin basal wall 0.02–0.03mm thick and diverge distally in the narrow endozone. At the exozone

they bend slightly and vestibules are orientated perpendicular to the zoarial surface. Chamber walls are only 0.01–0.02mm thick in the endozone, but are considerably thicker, ranging from 0.15–0.18mm, in the exozone. These endozonal walls are straight, and rarely moniliform.

Ring septa are developed within the exozone where generally three to four are found. (A greater number have been reported from solid ramose zoaria where the exozone is thicker (Lee 1912, Bancroft 1984)). The inner margins of the ring septa are unthickened, thin and not deflected posteriorly. Foramen are 0.08 to 0.12mm in diameter, centrally placed, and circular to occasionally reniform in shape.

Autozooecial apertures are large, and polygonal to infrequently circular in shape and are very closely spaced at less than one diameter apart. Exilazooecia are small, with circular apertures. They are uncommon, and usually occur as isolated individuals between autozooecia at interapertural angles.

Interapertural walls are very thin and angular or rounded with stylets developed along their crests. Large acanthostyles are found at interzooecial junctions, while as many as 20 smaller heterostyles may occur between them, around autozooecia. Acanthostyles reach 0.05mm in thickness and 0.09mm in length.

**Table 25** Measurements of *Tabulipora howsii* (in mm). N=14.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| MTZ | 41 | 0.45 | 0.24 | 1.30 | 9.10 | 3.31 |
| Z1 | 72 | 9 | 6 | 11 | 8.24 | 11.02 |
| Z2 | 74 | 6.41 | 5 | 8 | 7.74 | 10.48 |
| AD | 130 | 0.27 | 0.20 | 0.35 | 9.16 | 17.77 |
| IWT | 126 | 0.03 | 0.01 | 0.08 | 24.2 | 13.08 |
| FD | 35 | 0.09 | 0.06 | 0.12 | 11.19 | 7.31 |
| ED | 4 | 0.09 | 0.05 | 0.13 | – | 2.67 |

MTZ = Maximum thickness of adnate zoarium from basal wall to external surface.

DISCUSSION. *Tabulipora howsii* is easily recognised by its thick ramose zoaria which may reach a diameter of 20mm, its moniliform exozonal wall, the presence of numerous ring septa, and from the often polygonal to angular autozooecial apertures.

However, no ramose specimens were found; this is unusual as they have previously been recorded in large numbers (Lee 1912, Bancroft 1984). Adnate colonies of *T. howsii* have been reported from Scotland (Bancroft 1984) but these have not been examined in the present study.

The number of exilazooecia may vary greatly from zoaria to zoaria. In the County Fermanagh specimens exilazooecia are generally few in number. However, Bancroft (1984: 376) describes them as common, occurring as either scattered individuals or in maculae, in ramose zoaria from the Midland Valley of Scotland, which suggests that the Fermanagh specimens were young individuals which had not developed ramose branches characteristic of older colonies.

Smyth (1925: 150) noted a variety of the taxon from the Asbian of North Wales, and stated that it conformed in every aspect with Lee's diagnosis except in two features: 30 not 40 autozooecial apertures were contained in a 1cm line, and the foramen were oval not reniform. Within the Scottish and County Fermanagh *T. howsii* populations there is variation in these characters and they are not considered herein to merit varietal status. Examination of Smyth's material (TCD.R11a–g, TCD.21545a, b) shows it to lie within the variation range of *T. howsii* as given by Bancroft (1984).

STRATIGRAPHICAL RANGE. Lower Carboniferous (Asbian–Brigantian).

DISTRIBUTION. Rare, but recorded from Counties Fermanagh and Donegal (Wright *et al.* 1913), the Midland Valley of Scotland, northern England, and North Wales.

### *Tabulipora minima* Lee, 1912 Figs 71c, 79

1912 *Tabulipora minima* Lee: 164, pl.15, fig.21.
1987 *Tabulipora minima* Lee; Bancroft: 196.

LECTOTYPE. Herein designated GAGM 01-53 BYC (longitudinal section in thin section, figured by Lee, 1912).

MATERIAL. Three zoarial fragments, BMNH PD9650, BELUM K2182. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; K3474 Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria are erect, ramose, and composed of moderately robust sub-circular branches. Only two zoaria were examined; the larger measures 14.7mm in length. The nature of branch division is not known.

Autozooecia are budded from within the endozone. Autozooecial chambers are long, reaching a maximum length of 4.3mm in length. They diverge at low angles of less than 25° in the endozone, and hardly bend posteriorly at the exozone.

Endozonal walls are very thin, undulating or straight. The majority of the autozooecial tube is contained within the endozonal area. Consequently the axial ratio is high. The exozone is only 0.11–0.21mm wide, where chamber walls are of regular thickness. Three to occasionally four ring septa are found per autozooecium. They are thin, with a central circular foramen, and are found towards the top of the endozone and within the exozone.

Autozooecial apertures are large, oval to circular in shape and closely spaced at less than one diameter apart. Interapertural walls are thin and smooth.

Exilazooecia are small, and range in diameter from 0.06 to 0.13mm. They are circular to oval in shape and occur as scattered individuals or in small clusters between autozooecia.

Stylets are of one structural type only. Between 12 and 15 large acanthostyles 0.06mm in diameter surround autozooecial apertures. They are arranged on interapertural walls, with one consistently positioned at interapertural junctions.

**Table 26** Measurements of *Tabulipora minima* (in mm). N=2.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 11 | 2.57 | 1.80 | 3.36 | 4.16 | 2.71 |
| Z1 | 16 | 12.95 | 10 | 16 | 11.75 | 9.63 |
| Z2 | 16 | 4.71 | 4 | 5 | 9.83 | 28.99 |
| AD | 20 | 0.23 | 0.15 | 0.30 | 13.43 | 4.74 |
| IWT | 19 | 0.08 | 0.05 | 0.12 | 22.92 | 12.02 |
| ED | 7 | 0.09 | 0.06 | 0.13 | 19.52 | 3.18 |
| ET | 5 | 1.99 | 1.38 | 2.58 | 1.46 | 2.38 |
| TE | 12 | 0.17 | 0.11 | 0.21 | 13.33 | 8.24 |

DISCUSSION. *Tabulipora minima* is easily recognised by its moderately robust and often flattened branches, by the presence of a very thin exozone, and by the occurrence of a small number of ring septa in each autozooecium.

It is rare in the British Isles. Only Lee (1912) and Bancroft (1984) have previously recorded it. At Carrick Lough three specimens were recovered. Although one of these was silicified a considerable amount of internal detail, including ring septa, is preserved.

STRATIGRAPHICAL RANGE. Carboniferous (Viséan–Arnsbergian).

DISTRIBUTION. Only recorded from County Fermanagh, Yorkshire, and the Midland Valley of Scotland.

## Genus *STENOPHRAGMIDIUM* Bassler, 1952

TYPE SPECIES. *Stenophragma lobatum* Munro, 1912, by original designation from the Lower Carboniferous of Ravenstonedale, Cumbria (formerly Westmoreland), England.

REVISED DIAGNOSIS. Stenoporid with encrusting, rarely ramose zoaria. Encrusting zoaria commonly form flat adnate colonies or hollow erect dichotomising expansions on which monticules are regularly developed.

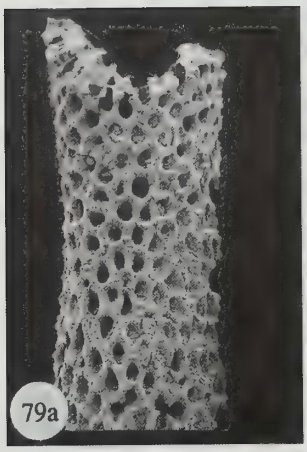
Autozooecial chambers have thickened walls in the exozone, where they are of uniform width or occasionally moniliform. Autozooecial chambers diverge distally at a low angle in the thin endozone, becoming perpendicular to the zoarial surface in the wider exozone. Up to five hemiphragms are developed on proximal walls, at the top of the endozone and in the exozone, where they extend halfway across chambers. Autozooecial apertures are of moderate size, circular to oval in shape, and closely spaced. Exilazooecia are rare.

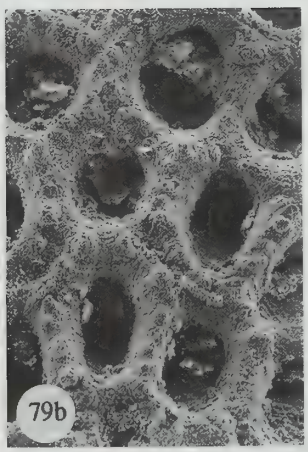
Large acanthostyles may be situated at zooecial wall junctions, and heterostyles may be disposed between them.

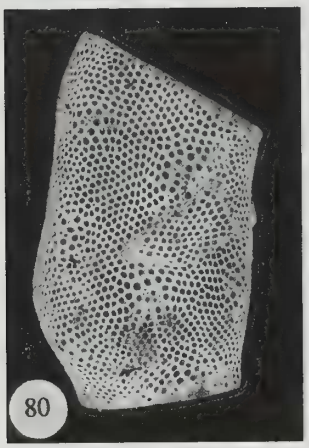
DISCUSSION. This genus, which is restricted to the Carboniferous, was first described from Northern England (Munro 1912). To date nineteen species have been reported; four species have been described from the Carboniferous of the British Isles. The British species are *Stenophragmidium grandyense* (Munro 1912), *S. lobatum* (Munro 1912) [the type species], *S. incrustans* Owen 1973 and *S. ramosum* Owen 1969. To these, five *Tabulipora* species of Lee (1912) may be added, as well as *Tabulipora serrata* Smyth, 1922 (from the Lower Carboniferous (Brigantian) of Ballycastle, County Antrim). They possess 'tabulae' which 'extend only partly, leaving an untabulated space, ... always situated on the distal side ...' (Lee 1912: 171). The 'tabulae' are clearly hemiphragms. Examination and revision of Lee's and Smyth's material may reveal that their six species are referable to *Stenophragmidium*.

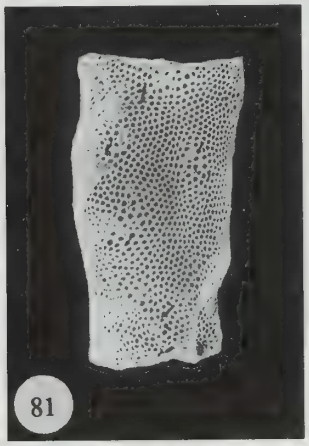
STRATIGRAPHICAL RANGE. Lower–Upper Carboniferous

DISTRIBUTION. British Isles, Belgium, the CIS (former Soviet Union), North America, Asia.



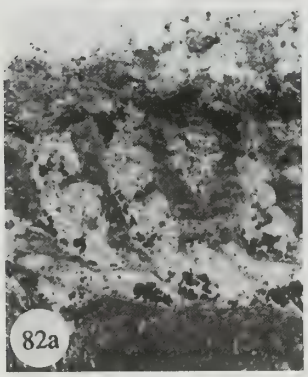





**Fig. 79** *Tabulipora minima* Lee, 1912; Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; BMNH PD9650; **79a,** portion of ramose colony showing arrangement of autozooecia with oval apertures, ×20; **79b,** detail of 79a, showing oval autozooecial apertures divided by thick interapertural walls on which are developed large acanthostyles, ×100.

**Figs 80–82** *Stenophragmidium* sp. Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh; **80,** BELUM K15209, ramose hollow zoarial fragment, with regular disposition of monticules and autozooecia; small exilazooecial apertures are found between autozooecia, particularly on monticules; autozooecia adjacent to monticules are larger than those in inter-monticular areas, ×3; **81,** BELUM K15210, zoarial fragment, details as for 80, ×2.5; **82,** BELUM K15214; **82a,** longitudinal section through colony showing thin undulatory basal wall, low angle of divergence of autozooecia in endozone, increasing in exozone region; chamber walls thin in endozone, thicken rapidly in exozone; a single hemiphragm is situated on proximal chamber walls, bends inwards, and seals half the vestibule; ×25; **82b,** detail of 82a, ×75.

***Stenophragmidium*** sp. Figs 80–83

MATERIAL. BELUM K3436, K15209-K15215 (5 zoarial fragments and 2 longitudinal sections), Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria consist of large erect hollow expansions up to 11.17mm in width, or thin encrusting adnate sheets 0.28–0.30mm thick. Autozooecia are budded from a very thin undulating basal wall. Autozooecial chambers are recumbent in the thin endozonal region (0.15 mm) and straight in the wider exozone (0.28 mm). The vestibule lies at a high angle of 80° to 85° to the zoarial surface, and is moderately wide (0.19–0.20 mm).

Autozooecial walls are 0.03–0.04 mm thick in the endozone, but expand rapidly in the exozone to between 0.15 and 0.18 mm. They are usually of constant width, occasionally undulatory, and rarely moniliform. Walls consist of a well defined central hyaline zone (0.02 mm wide) in which laminae are orientated parallel to the growth direction. Thin lateral laminae are derived from this central zone and bend sharply proximally. This is typical leioclemid-type wall structure (after Boardman 1960).

Up to three hemiphragms are developed within and at the base of the exozone, where they arise from proximal walls. They are thin, often straight and occasionally bend slightly proximally. They are short (0.04–0.07 mm in length), usually extend less than half-way into chambers, and have rounded bulbous tips.

Autozooecial apertures are polygonal or irregular in shape, occasionally circular and are closely spaced at less than one diameter apart. Apertures decrease in diameter away from monticules. Interapertural walls are rounded and moderately thick, with as many as 16 stylets occurring along their crests.

Large acanthostyles (0.05–0.07 mm) are usually found at autozooecial wall junctions, with smaller stylets (0.02–0.03 mm) between. Exilazooecia are rare; they are small, with circular to angular apertures. They occur as isolated individuals between autozooecia, or infrequently in groups of 10 to 12 in monticule-centred maculae which are widely spaced at up to 5.53 mm apart.

DISCUSSION. This taxon is known from 14 specimens from which details of both external and internal structure are known. It does not resemble previously described British species, but may be synonomous with *Tabulipora crassimuralis* Lee, 1912. The genus needs revision, which will be undertaken at a future date and until then I prefer to leave this taxon unassigned to any species.

The hollow portions of the zoaria examined all had a posthumous infill of micritic mud which was also found in autozooecial chambers. Zoaria possibly encrusted soft algal branches which have now disappeared, or may simply have been hollow.

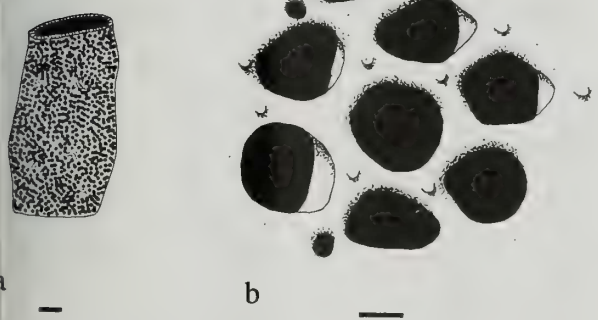



**Fig. 83** *Stenophragmidium* sp. Line drawing of external features of BELUM K15209; **a,** Portion of hollow ramose colony, scale bar = 1 mm; **b,** detail of autozooecia and exilazooecia and disposition of acanthostyles, scale bar = 0.1 mm.

**Table 27** Measurements of *Stenophragmidium* sp. (in mm). N=6.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| ZD | 39 | 7.92 | 4.81 | 11.17 | 11.28 | 4.38 |
| Z1 | 60 | 7.73 | 5 | 10 | 12.08 | 13.44 |
| Z2 | 60 | 5.5 | 4 | 8 | 13.39 | 6.16 |
| AD | 60 | 0.24 | 0.15 | 0.32 | 10.75 | 10.84 |
| IWT | 60 | 0.07 | 0.04 | 0.12 | 20.86 | 7.96 |
| ED | 60 | 0.08 | 0.06 | 0.15 | 21.26 | 7.55 |
| ET | 4 | 0.64 | 0.25 | 1.07 | 10.60 | 1.22 |
| TE | 4 | 1.64 | 0.90 | 2.76 | 16.76 | 1.68 |
| IMS | 6 | 4.45 | 3.38 | 5.53 | 18.34 | 14.30 |

STRATIGRAPHICAL RANGE. Lower Carboniferous (Viséan, Asbian).

DISTRIBUTION. Ireland, North Wales.

Order **CYSTOPORATA** Astrova, 1964
Suborder **FISTULIPORINA** Astrova, 1964
Family **FISTULIPORIDAE** Ulrich, 1882
Genus ***FISTULIPORA*** M'Coy, 1849

TYPE SPECIES. *Fistulipora minor* M'Coy, 1849 by subsequent designation (Milne-Edwards & Haime 1850: lix) from the Lower Carboniferous of the British Isles.

***Fistulipora incrustans*** (Phillips, 1836)
Figs 84a, 85–88, 105

A complete systematic description, full synomony and discussion of the type specimens is given in Bancroft & Wyse Jackson (1995).

MATERIAL. BMNH PD9651-9676, 9740; TCD.34088-34103, 34138-34139, 34146, 34157, 34159, 34166, 42590, 42610; BELUM K2151, K2153, K2193, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42511, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria form thin unilaminate button-like discs up to 1.3cm in diameter; encrusting unilaminate or multilaminate sheets up to 1.58mm thick, or small chaetetiform nodular expansions 30mm wide by 17mm high. Colonies often encrust crinoid stems, fenestellid Bryozoa, and occasionally brachiopod valves.

Autozooecia are budded from a very thin basal wall (0.015–0.025 mm thick). They are often initially slightly recumbent, but subsequently become erect and orientated at 80° to 90° to the zoarial surface. Autozooecia are straight, tubular and thin walled. Thin diaphragms are commonly developed at the base of chambers and are less common and irregularly dispersed throughout the remaining portions of chambers. Autozooecia are arranged in straight to curved rows which produces an offset pattern on the zoarial surface. Autozooecial apertures are large (0.17mm to 0.40mm); usually circular to oval, occasionally D-shaped, rarely sub-polygonal in shape and spaced 1–2.5 diameters apart. Lunaria are indistinct and not consistently present. They are small – only one fifth the circumference of apertures, crescent-shaped, marginally elevated above the zoarial surface, and discretely indent apertures (by as much as 0.04mm). Lunaria are found on the proximal sides of autozooecia closest to monticules. In a few zoaria lunaria completely encircle autozooecial apertures, forming low peristome-like collars. Rarely,

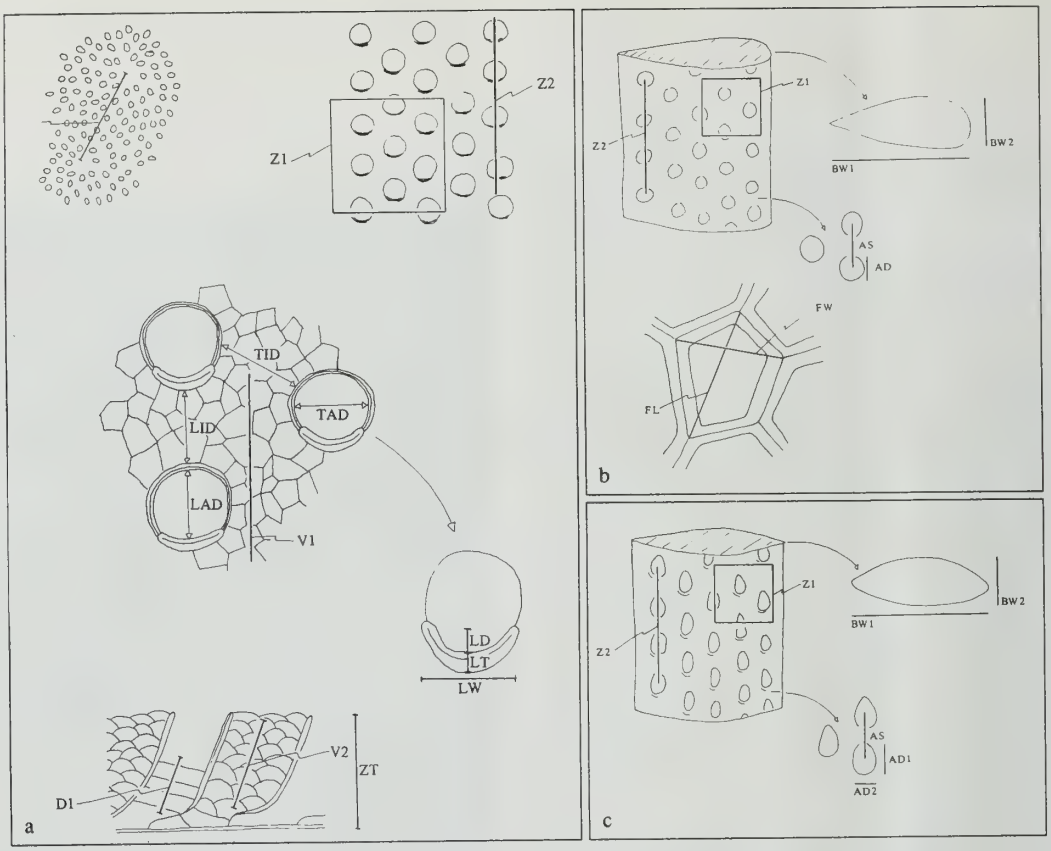



**Fig. 84** Measurements taken on cystoporates in this study; **a,** *Fistulipora incrustans* (Phillips, 1836); **b,** *Sulcoretepora parallela* (Phillips, 1836); **c,** *Goniocladia cellulifera* (Etheridge, 1873b); ZT = Zoarial thickness from basal wall to upper zoarial surface; BW1 = Branch width measured parallel to median wall; BW2 = Branch width measured perpendicular to median wall; MS = Distance between adjacent monticule measured from centre to centre; V1 = Number of vesicles contained along a 1mm line; FL = Fenestrule length; FW = Fenestrule width; AD1 = Autozooecia apertural diameter measured parallel to growth direction; AD2 = Autozooecia apertural diameter measured perpendicular to growth direction; AS = Autozooecia apertural spacing: minimum distance between two adjacent autozooecial apertures, measured from their centres; LAD = Autozooecia apertural length measured from lunaria to opposite side; TAD = Autozooecia apertural width measured perpendicular to LAD; LID = Autozooecia apertural spacing in same longitudina row; TID = Autozooecia apertural spacing between adjacent rows; Z1 = Number of complete autozooecial apertures contained in 1 $mm^2$; Z2 = Number of complete autozooecial apertures contained in a 2mm line; LW = Lunarium width; LT = Lunarium thickness; LD = Lunarium depth; V2 = Number of vesicles seen in transverse section contained along a 1mm line; D1 = Number of diaphragms contained within 1mm.

large hood- or cowl-like lunaria are developed. These are 0.1 mm high and cover approximately half the aperture. They are similar to those illustrated by Warner & Cuffey (1973) in *F. incrustans* Moore and *F. carbonaria*.

Monticules are regularly arranged between 2 and 5mm apart and are conspicuously elevated above the general surface of zoaria. Small maculae (*sensu* Anstey 1981) are found at the apex of each monticule. Autozooecia develop in intersecting semi-circular rows away from monticules.

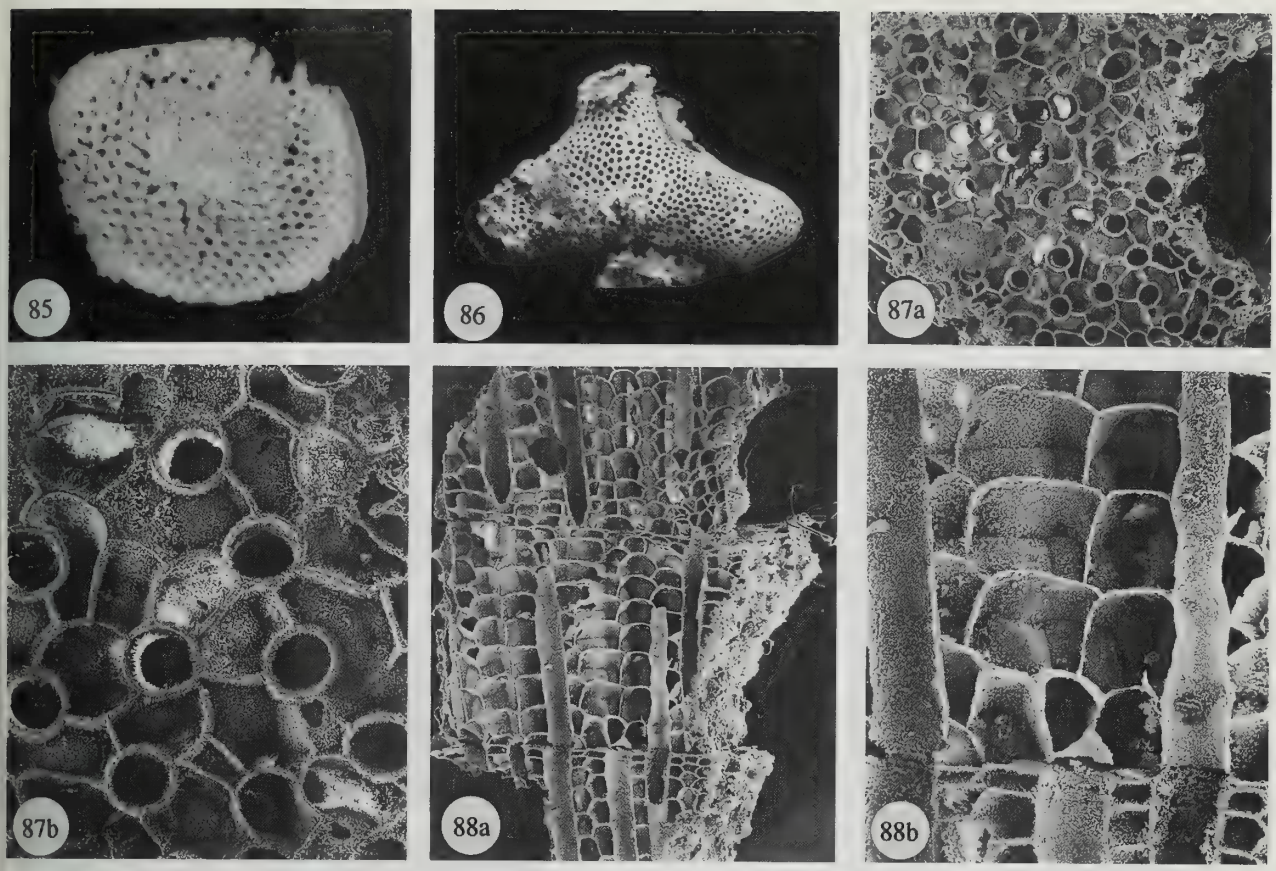
Vesicles are arranged in 3 to 4 vertical stacks between autozooecia, with 5–8 contained within 1mm per stack. They are small, rectangular, polygonal or inverted cup-like structures. They become increasingly thinner towards the zoarial surface. Between ten and fifteen vescicles are found in each vertical stack.

In some large colonies five to six encrusting cycles have been seen (this is not unusual – many more such multilaminate sheets have been observed in massive colonies from other localities).

DISCUSSION. *Fistulipora incrustans* is easily recognised by its encrusting habit, its large circular autozooecial apertures, its stacked interzooecial vesicular tissue, and by the regular monticular a rangement.

**Table 28** Measurements of *Fistulipora incrustans* (in mm). N=15.

| | NM | x | Mn | Mx | CVw | CV |
|---|---|---|---|---|---|---|
| ZT | 41 | 0.67 | 0.20 | 1.58 | 18.10 | 1.( |
| AD | 119 | 0.27 | 0.18 | 0.40 | 10.73 | 6.( |
| LAD | 20 | 0.24 | 0.20 | 0.32 | 10.10 | 11.5 |
| TAD | 20 | 0.30 | 0.17 | 0.36 | 15.74 | 17.1 |
| AS | 115 | 0.28 | 0.10 | 0.55 | 23.64 | 4. |
| LID | 20 | 0.41 | 0.22 | 0.66 | 22.42 | 2.3 |
| TID | 20 | 0.27 | 0.20 | 0.45 | 14.59 | 4. |
| Z1 | 117 | 3.5 | 2 | 6 | 16.88 | 6. |
| Z2 | 109 | 3.9 | 3 | 6 | 11.75 | 7. |
| V1 | 16 | 4.6 | 3 | 6 | 16.04 | 5.( |
| V2 | 20 | 5.4 | 3 | 8 | 16.60 | 6.3 |
| MS | 8 | 2.88 | 0.63 | 4.92 | 12.21 | 1. |
| LW | 18 | 0.20 | 0.17 | 0.23 | 7.84 | 20. |
| LD | 12 | 0.01 | 30.0 | 10.02 | 29.25 | 3. |
| LT | 12 | 0.03 | 0.02 | 0.07 | 23.12 | 3. |




**Figs 85–88** *Fistulipora incrustans* (Phillips, 1836); Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **85,** BMNH PD9651, small dome-shaped adnate zoarium (encrusting *Baculopora megastoma* fragment) showing regular arrangement of autozooecia in curved intersecting rows; lunaria are situated on the upper edges of apertures, ×10; **86,** BMNH PD9652, chaetetiform colony showing monticular arrangement, ×3.5; **87,** BMNH PD9676; **87a,** transverse view of circular autozooecial apertures separated by vesicular tissue, ×20; **87b,** detail of 87a, ×60; **88,** BMNH PD9675; **88a,** longitudinal section showing three growth increments, simple tubular autozooecial chambers, and vesicular tissue comprising box-like vesicles with domed upper surfaces, ×20; **88b,** detail of 88a, ×60.

It is the only species of *Fistulipora* described from the British Isles. Several previously reported taxa are considered synonymous with it. These are *Fistulipora minor* M'Coy, 1849 (see Owen 1969), and *Berenicea megastoma* M'Coy, 1844, which Young (1882) considered to be an immature *F. incrustans* colony (Bancroft & Wyse Jackson 1995).

*F. excelens* Ulrich, 1884, has a similar form and morphometric measurements to *F. incrustans* (Phillips, 1836) and might be synonymus. *F. incrustans* Moore (1929) (a secondary homonym) from Texas has significantly larger elliptical to oval-shaped autozooecial apertures, which are surrounded by complete peristomes, and is not conspecific. On the other hand, the specimens described as *F. incrustans* Moore by Warner & Cuffey (1973) from the Lower Permian of Kansas are similar in most respects, and are probably conspecific with *F. incrustans* (Phillips, 1836).

Some morphological variation is seen both within and between colonies although this is not as considerable as the variation recorded by Warner & Cuffey (1973). They measured parameters in which high variation would be expected (eg. lunaria width and cystopore dimensions). In this study a smaller number of parameters were measured: these are associated with the autozooecia (eg. autozooecial chamber width and spacing) and variation in them is thought to be indicative of minor environmental changes (Farmer & Rowell 1973).

STRATIGRAPHICAL RANGE. Lower Carboniferous (Courceyan)–Lower Permian.

DISTRIBUTION. *Fistulipora incrustans* is a common species with a wide geographical range. It is frequent in the Lower Carboniferous of the British Isles, and has been recorded from the CIS (former Soviet Union), and North America.

## Family **CYSTODICTYONIDAE** Ulrich, 1884
## Genus ***SULCORETEPORA*** d'Orbigny, 1849

TYPE SPECIES. *Flustra? parallela* Phillips, 1836 by original designation from the Lower Carboniferous of Whitewell, Yorkshire, England.

REVISED DIAGNOSIS. Cystodictyonid with erect zoaria composed of dichotomising bifoliate branches, elliptical to oval in cross-section. Branches retain a constant width along their length. Autozooecia are budded from a straight or zig-zag median wall

which is composed of a dark central granular skeleton surrounded by laminated skeleton. Autozooecia are arranged in longitudinal rows. Zooecial chambers are long and narrow in the endozone and bend sharply in the exozone. In tangential section, chambers are rectangular in shape. Vesicles are found in the outer endozone and inner exozone, where they occur as irregular to circular cavities. They become less abundant towards the zoarial margin. Indistinct lunaria are found on the proximal edge of the large oval-shaped autozooecial apertures. Interapertural areas are smooth with a single longitudinal ridge developed between adjacent autozooecial rows.

DISCUSSION. Taxonomically *Sulcoretepora* has presented many problems and prompted much argument. At ordinal level it was first regarded as a cryptostome (Vine 1884a), and this view was maintained until recently (Cuffey 1973). It is now recognised as a cystoporate (Morozova 1970, Utgaard 1983). At generic level *Sulcoretepora* was first described by d'Orbigny (1849), who designated Phillip's species *Flustra? parallela* as type species. Subsequently, Ulrich (1882) erected the genus *Cystodictya* (type species, *C. ocellata* from the Mississippian of Somerset, Kentucky, U.S.A.) and placed *Sulcoretepora* in synonymy with it on account of the shared presence of a median wall. Many authors have followed this opinion (eg. Young 1887, Vine 1888). Close examination of the two genera shows that there is a difference in the shape and nature of the median wall. It is always straight in *Cystodictya*, but is undulatory or sharply folded in *Sulcoretepora*. *Mstainia* Shulga-Nesterenko, 1955, has a plicated median wall and is regarded a junior subjective synonym of *Sulcoretepora* (Elias 1964).

STRATIGRAPHICAL RANGE. Devonian–Permian.

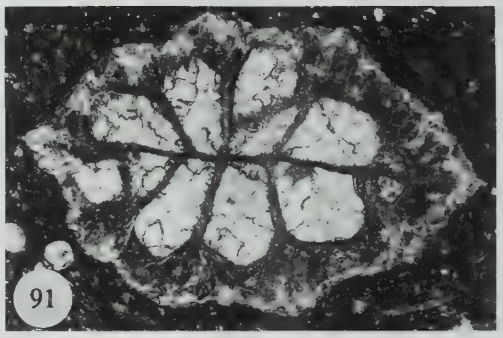
DISTRIBUTION. British Isles, Europe, the CIS (former Soviet Union), United States, Asia.

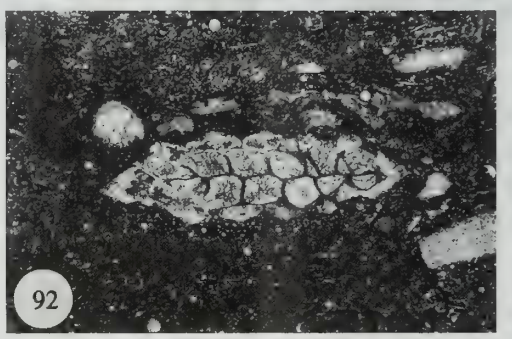
***Sulcoretepora parallela*** (Phillips, 1836) Figs 84b, 89–93

| | |
|---|---|
| 1836 | *Flustra? parallela* Phillips: 200, pl.1, figs 47, 48. |
| 1843 | *Flustra? parallela* Phillips; Morris: 37. |
| v1844 | *Vincularia parallela* (Phillips); M'Coy: 198, pl. 27, fig. 14. |
| 1849 | *Sulcoretepora parallela* (d'Orbigny); d'Orbigny: 152. |
| 1854 | *Sulcoretepora parallela* (d'Orbigny); Morris: 105. |
| 1862 | *Vincularia parallela* (Phillips); Griffith: 227. |
| 1877 | *Sulcoretepora parallela* (Phillips); Vine: 273. |
| 1880c | *Ptilodictya? parallela* (Phillips); Vine: 508. |
| 1884a | *Arcanopora parallela* (Phillips); Vine: 204. |
| 1885 | *Cystodictya parallela* (Phillips); Vine: 95. |
| 1887 | *Cystodictya parallela* (Phillips); Young: 461. |
| 1888 | *Cystodictya parallela* (Phillips); Vine: 74. |
| 1953 | *Sulcoretepora parallela* (Phillips); Bassler: 142, fig. 103. |
| 1964 | *Sulcoretepora parallela* (Phillips); Elias: 380, pl. 5, figs 3–6. |
| 1969 | *Sulcoretepora parallela* (Phillips); Owen: 265, pl. 23, figs E–F. |
| 1983 | *Sulcoretepora parallela* (Phillips); Utgaard: 429, fig. 210, 1a–f. |
| 1986a | *Sulcoretepora parallela* (Phillips); Bancroft: 23. |
| 1987 | *Sulcoretepora parallela* (Phillips); Bancroft: 196. |
| 1991 | *Sulcoretepora parallela* (Phillips); Billing: 41. |

MATERIAL. BMNH PD9563, 9619, 9677-9700; TCD.34104-34111, 34138, 34142, 34146, 34148-34153, 34157-34158, 34172, 42596, 42600b, 42605; BELUM K2158. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh.






**Figs 89–92** *Sulcoretepora parallela* (Phillips, 1836); Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **89,** BMNH PD9677, branch fragment showing arrangement of autozooecia in longitudinal rows separated by longitudinal ridges, ×15; **90,** BMNH PD9678, as 89; lunaria are more pronounced proximally of autozooecial apertures; the size and spacing of autozooecial apertures increases in rows from left to right, ×15; **91,** BMNH PD9619, transverse section showing scalloped branch margins, atypical straight median wall, and elongate polygonal autozooecial chambers with rounded lateral margins, ×50; **92,** BMNH PD9563, transverse section with more typical plicated median wall, ×20.

TCD.42555-42558, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

DESCRIPTION. Zoaria form quite large expansions of dorsoventrally flattened branches that are elliptical or oval in cross-section. Bifurcation of branches is more common than the development of lateral branches, which are thinner than the main branch. The largest fragment measured is 38.8mm in length and no lateral branches

**Fig. 93** *Sulcoretepora parallela* (Phillips, 1836). Line drawing of external features of BMNH PD9678; scale bar = 1 mm.

were developed. Mature branches are usually of constant width along their length, but a small amount of thinning distally can occur. The ratio of branch thickness (BW2) to branch width (BW1) ranges from 1:4 to 1:2.

Autozooecia are arranged in 4 to 6 longitudinal rows on the lateral sides of branches. The number of longitudinal rows remains constant along the length of a branch. Autozooecial apertures are of medium to large size and circular to oval in shape. A thin proximal lunarium is present around each autozooecial aperture. Apertures are spaced two and a half to three diameters apart. This spacing increases slightly in the rows adjacent to the median ridge. Here three autozooecial apertures generally occur in a 2mm line, while four occur in the same length in rows away from the median ridge. Between adjacent rows of autozooecial apertures a strong narrow longitudinal ridge is developed. A smaller, fainter ridge is often found either side of the main ridge. This second ridge is found between the distal and proximal ends of two autozooecial apertures in the same row. The interapertural areas are smooth except for the longitudinal ridges.

Branches are internally divided by a thin plicated median wall, from either side of which are budded autozooecia. The median wall is composed of pale laminated skeletal material.

Autozooecial chambers are elongate, narrow, and bend distally in the endozone region. The exozone is extremely thin, being about one sixth the thickness of the branch. Autozooecial chamber walls are thin and straight. In shallow tangential section chambers are tear-shaped and narrower proximally. Deeper sectioning shows the chambers to have a rectangular shape. In cross-section chambers are hexagonal to pentagonal in outline.

Small vesicles, 0.03 mm in diameter, are commonly found between autozooecial chambers and the branch margin. They are most frequently developed in the outer endozone and inner exozone. They are thin-walled, circular to irregular in shape, and may be infilled with stereom in the exozone.

**Table 29** Measurements of *Sulcoretepora parallela* (in mm). N=21.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW1 | 172 | 1.02 | 0.68 | 1.43 | 4.39 | 5.34 |
| BW2 | 38 | 0.49 | 0.31 | 0.75 | 7.92 | 3.14 |
| Z1 | 63 | – | 6 | 8 | 8.46 | 19.38 |
| Z2 | 170 | – | 3 | 4 | 11.57 | 23.28 |
| AD1 | 200 | 0.19 | 0.11 | 0.29 | 9.90 | 6.70 |
| AD2 | 201 | 0.12 | 0.08 | 0.20 | 11.49 | 6.64 |
| AS | 201 | 0.56 | 0.38 | 0.82 | 10.72 | 11.72 |

DISCUSSION. *Sulcoretepora parallela* is unmistakable in appearance due to its strap-like branches with a regular arrangement of autozooecial apertures which are divided by longitudinal ridges. This bryozoan displays very little variation either within or between colonies in a population. Computed coefficients of variation for branch width (BW1), branch thickness (BW2), and autozooecial apertural diameter (AD1 and AD2) are all very low. The values for the other parameters, those that are a measure of autozooecial spacing (Z1, Z2, and AS), are higher, but are still regarded as low when compared with other bryozoan taxa.

*Sulcoretepora parallela* has a wide distribution in the Carboniferous of the British Isles. It is common in the Carrick Lough/Sillees River assemblage.

Three other species of *Sulcoretepora* have been described from the Carboniferous of the British Isles: *S. ramosa* Owen 1973, *S. raricosta* (M'Coy, 1844), and *S. robertsoni* (Young & Young, 1877). *S. ramosa* is not a sulcoreteporid but is a hyphasmoporid cryptostome. Branches are circular and not bifoliate, it lacks a median wall and lunaria, and acanthostyles are common. It occurs in County Fermanagh and is redescribed herein as *Clausotrypa ramosa* (Owen, 1973).

The other species of *Sulcoretepora* differ from *S. parallela* in a number of respects. *S. raricosta* has autozooecia of similar dimensions to those in *S. parallela* but has more autozooecia developed on one side of the branch than the other. Branches of *S. robertsoni* are nearly circular in cross-section, autozooecial apertures are larger, and interapertural areas are pitted and more ornate (Young & Young 1877).

STRATIGRAPHICAL RANGE. Carboniferous (Holkerian–Pendleian).

DISTRIBUTION. British Isles.

## Family **GONIOCLADIIDAE** Waagen & Pichl, 1885
## Genus ***GONIOCLADIA*** Etheridge, 1876

TYPE SPECIES. *Carinella cellulifera* Etheridge, 1873, by original designation from the Lower Carboniferous of Carluke, Scotland.

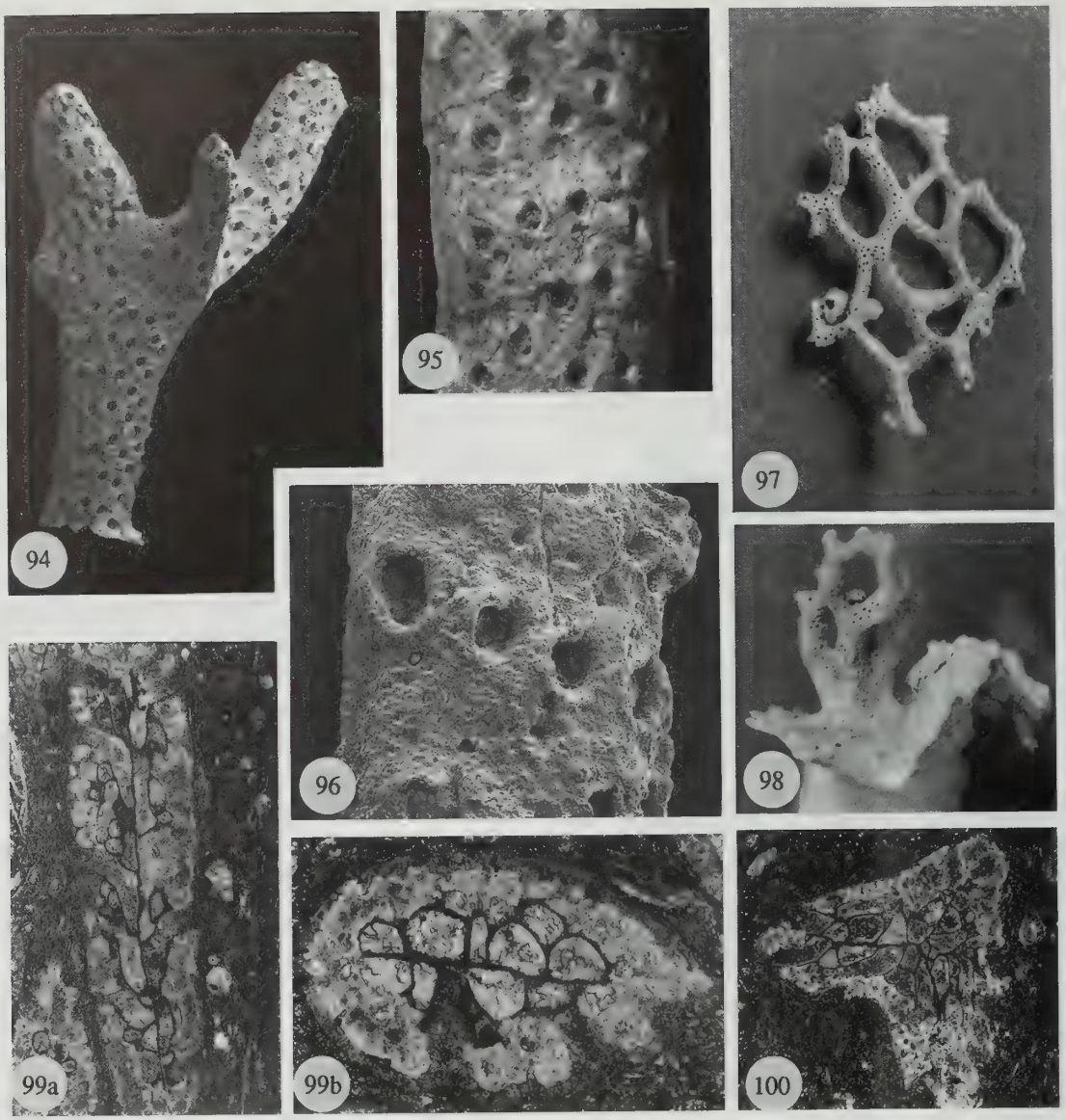
### ***Goniocladia cellulifera*** (Etheridge, 1873)

Figs 84c, 94–102

1873a *Carinella cellulifera* Etheridge: 433.
1873b *Carinella cellulifera* Etheridge; Etheridge: 101.
1876 *Goniocladia cellulifera* (Etheridge); Etheridge: 522.
1880b *Goniocladia cellulifera* (Etheridge); Vine: 81.
1880c *Goniocladia cellulifera* (Etheridge); Vine: 507.
1885 *Goniocladia cellulifera* (Etheridge); Waagen & Pichl: 804.
1887 *Goniocladia cellulifera* (Etheridge); Young: 463.
1888 *Goniocladia cellulifera* (Etheridge); Vine: 77.
1888 *Goniocladia cellulifera* (Etheridge) var. *robusta* Vine: 78.
1953 *Goniocladia cellulifera* (Etheridge); Bassler: 89, fig. 54.
1983 *Goniocladia cellulifera* (Etheridge); Utgaard: 434, figs 213, 1a–h.
1986a *Goniocladia cellulifera* (Etheridge); Bancroft: 23.
1987 *Goniocladia cellulifera* (Etheridge); Bancroft: 196.

MATERIAL. BMNH PD9563, 9701, 9703-9721; TCD.34112-34120, 34135, 34146-34147, 34150-34154, 34157, 42589, 42600a, 42602b, 42604a, 42606c; BELUM K2162-5, K12003, Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh. TCD.42512, Upper part of the Glencar Limestone (Viséan, Asbian), Sillees River, County Fermanagh.

EMENDED DIAGNOSIS. *Goniocladia* with large reticulate or occasionally adnate zoaria composed of bifoliate straight to gently curved branches. Branches anastomose at regular intervals to form




**Figs 94–100** *Goniocladia cellulifera* (Etheridge, 1873b); Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh; **94,** BMNH PD9719, colony fragment with typical branching pattern at a triple point, ×9; **95,** BMNH PD9704, laterally flattened branch with sharp median ridge on left and rounded carinal ridge on right; autozooecia are arranged in longitudinal rows with circular apertures: lunaria are indistinct; cystopores open to the surface and are seen as small circular 'pits' in interapertural areas, ×50; **96,** BMNH PD9718, close-up of branch with circular autozooecial apertures and small cystopore-openings, ×45; **97,** BELUM K2164, portion of reticulate colony. Branches divided perpendicular to the plane of the median wall; they coalesce to form large open rhombic, polygonal to irregularly-shaped fenestrules, ×6; **98,** BELUM K2163, robust holdfast of colony with portion of branch reticulation, ×6; **99,** BMNH PD9721; **99a,** longitudinal section. Autozooecia diverge from a planar thin median wall at low angles; chambers are separated by vesicular tissue which consists of irregular to spherical vesicles, ×20; **99b,** transverse section; the carinal ridge is on the left hand side while the sharper median ridge forms a sharp keel on the right. Autozooecia are polygonal, squat, and the median wall is straight, ×40; **100,** BMNH PD9563, transverse section through a triple point reflected by the division of the median wall, ×20.

large pentagonal or polygonal fenestrules. In cross-section branches are pyriform. They are bisected by a compound median wall which protrudes as a faint carina on the rounded barren surface and as a strong keel on the obverse surface.

Autozooecia are large, circular and arranged in quincunx in four to seven longitudinal rows either side of the median wall, from which they are budded. Low indistinct lunaria are frequently developed around autozooecial apertures. Interapertural areas are smooth. Autozooecial chambers are narrow, recumbent, and closely packed in the endozone. They diverge away from adjacent chambers in the exozone, and vestibules are orientated at a high angle to the zoarial surface. Autozooecial chamber walls are thin. Basal diaphragms are rare.

DESCRIPTION. Zoaria form large planar reticulate colonies of unknown maximum dimensions. The largest reticular fragment

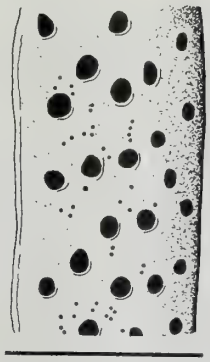


**Fig. 101** *Goniocladia cellulifera* (Etheridge, 1873b). Line drawing of external features of BMNH PD9704; scale bar = 1 mm.

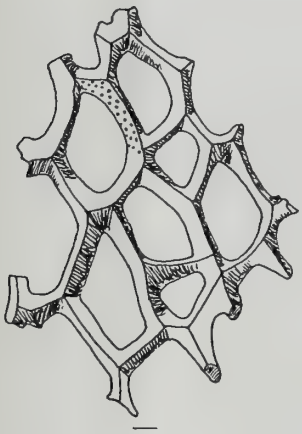


**Fig. 102** *Goniocladia cellulifera* (Etheridge, 1873b). Line drawing of protion of a reticulate colony of BELUM K2164; scale bar = 1 mm.

examined measured 19 × 12mm. Branches are bifoliate, laterally flattened, straight, and maintain a constant width along their length except prior to division when a small increase in width occurs. Branches divide, at angles of 30° to 70°, at short regular intervals. Coalescing of branches produces a regular pattern of pentagonal, hexagonal, or polygonal fenestrules upto 4.9mm long by 3.4mm wide. Branch division frequently produces three branches 60° apart. Dissipiments are absent.

Branch cross-sections are narrow with a pyriform to rhombic outline. The barren reverse surface is well rounded with a faint to distinct longitudinal carina while the celluliferous frontal surface is divided by a strong narrow angular median keel. These ridges are the external manifestations of the internal median wall.

Autozooecial apertures are arranged in quincunx in four to seven longitudinal rows, either side of the median ridge. Autozooecial apertures are large, circular to rarely oval in shape. Proximal lunaria are developed around most apertures. The size and thickness of the lunaria decreases towards the median keel. Interapertural areas are smooth and featureless. Autozooecial apertures are regularly spaced within longitudinal rows. Interapertural spacing decreases towards the median keel from five to two diameters apart (Table 31 and Fig. 103).

Colonies arise from stout holdfasts up to 13mm in width. Initial colony growth is encrusting where autozooecial apertures are large, circular in shape and closely spaced. From this adnate portion three to six erect branches arise, which either remain isolated as erect eschariform colonies or anastomose to form reticulate colonies.

Internally branches are divided by a thin, straight compound median wall. It is composed of a dark coarse central layer surrounded by a thin pale laminated layer. Autozooecia are budded from this wall. In the endozone autozooecial chambers are long, narrow, recumbent, and the thin chamber walls are shared. In transverse section they are semi-circular to pentagonal in shape. Autozooecial chambers curve distally from the median wall at angles of between 60° and 20°, and they diverge away from each other so that in the exozone they are isolated. The thickness of the exozone is greatest at the widest portion of the branch, where vestibules are oriented at a high angle to the zoarial surface, and decreases in the autozooecial rows towards the median keel, where vestibules lie at a low angle to the zoarial surface.

Small hemispherical vesicles 0.01 to 0.03mm in diameter are commonly found between autozooecial chambers. They are thin-walled, irregularly shaped and may be infilled with stereom in the endozone.

**Table 30** Measurements of *Goniocladia cellulifera* in mm. N=18.

| | NM | x | Mn | Mx | CVw | CVb |
|---|---|---|---|---|---|---|
| BW1 | 137 | 1.47 | 0.83 | 2.30 | 7.38 | 5.00 |
| BW2 | 44 | 0.69 | 0.33 | 0.98 | 9.03 | 6.21 |
| Z1 | 62 | 6.30 | 4 | 9 | 13.06 | 12.01 |
| Z2 | 161 | 3.90 | 2 | 6 | 15.17 | 9.41 |
| AD | 180 | 0.12 | 0.10 | 0.20 | 11.73 | 10.28 |
| AS | 178 | 0.57 | 0.32 | 1.12 | 24.90 | 7.35 |
| FL | 7 | 4.91 | 3.69 | 6.56 | 21.30 | –1 |
| FW | 7 | 3.40 | 2.56 | 4.40 | 17.89 | – |

**Table 31** Differences in apertural spacing in longitudinal rows in *Goniocladia cellulifera* (in mm).

| | Carinal ridge (barren surface) | | | | | | >Median keel (obverse surface) |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| NM | 13 | 13 | 13 | 12 | 12 | 10 | 5 |
| Mn | 0.73 | 0.52 | 0.43 | 0.42 | 0.39 | 0.33 | 0.47 |
| Mx | 1.12 | 1.04 | 1.00 | 1.02 | 1.00 | 0.73 | 0.75 |
| x | 0.86 | 0.71 | 0.64 | 0.61 | 0.59 | 0.55 | 0.53 |

DISCUSSION. *Goniocladia cellulifera* is quite common in the Lower Carboniferous of the British Isles, where it has been described from the Midland Valley of Scotland, Cumbria, Northumberland, and Yorkshire. It is very distinct with an unusual laterally flattened branch bearing a number of rows of autozooecial apertures and a sharp median ridge.

It was first described as *Carinella cellulifera* by Etheridge (1873a), but he later realised that that generic name was pre-occupied by a nemertean worm, and so proposed the name *Goniocladia* (Etheridge 1876). He suggested (Etheridge 1873a, 1873b), on the evidence of external features, that *Goniocladia* was an intermediate between *Polypora* M'Coy and *Fenestella* Lonsdale. While *Goniocladia* does possess a median keel (as in *Fenestella*) and has more than two rows of autozooecial apertures (as in *Polypora*), internally it resembles neither. In *Goniocladia* the zoarium is divided into two by a straight

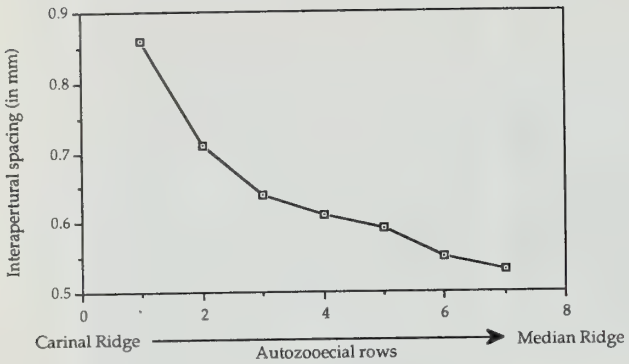



**Fig. 103** *Goniocladia cellulifera* (Etheridge, 1873b). Graph of apertural spacing.

vertical median wall from which autozooecia are budded; *Fenestella* and *Polypora* have no such median wall. Autozooecia in these two genera are budded from a basal wall.

STRATIGRAPHICAL RANGE. Lower Carboniferous.

DISTRIBUTION. British Isles.

## PALAEOECOLOGY OF THE COUNTY FERMANAGH BRYOZOAN FAUNA

The silicified Viséan fauna found towards the top of the Glencar Limestone has proved to be very diverse. It has been the subject of a number of research papers: the bryozoan element of the fauna has been systematically described by Bancroft & Wyse Jackson (1995), Olaloye (1974), Tavener-Smith (1965a, 1965b, 1971, 1973), Wyse Jackson (1988) and Wyse Jackson & Bancroft (1995a); the brachiopods by Brunton (1966a, 1966b, 1968, 1984); and the sponges by Reid (1970). These workers have recorded a large number of taxa (Tables 32 and 33). Other palaeontological work includes that of Gardiner & Mason (1974) who reported the occurrence of palaeoniscid fish from strata just overlying the Glencar Limestone, at a nearby locality west of Carrick Lough.

The fauna in County Fermanagh is essentially a bryozoan-brachiopod assemblage with rare taxa of other groups, such as trilobites, gastropods, bivalves, sponges and corals. This community is similar to that developed on the slopes of Asbian reefs of the Cracoe area, Yorkshire (Mundy 1978). Brunton (1987) tabulated the diverse and abundant fauna from Carrick Lough and Sillees River (Table 33). The number of bryozoan species described has been increased in this paper, and Bryozoa are now the largest element (numerically by species) in the community. The bryozoan fauna is dominated by fenestrates, which in turn are dominated by fenestellids. However, the delicate cryptostomes are also quite common (Table 32).

During this study one blastoid species and one ostracod species not recorded by Brunton (1987) have been found. Three specimens of the blastoid *Monoschizoblastus rofei* (TCD.9605), common in Asbian strata (Waters & Sevastopulo 1984a, 1984b), and one specimen of the ostracod *Polytylites* (TCD.9606) complete with both left and right valves were found.

**Table 32** List of bryozoans from the Lower Carboniferous (Viséan, Asbian) of Carrick Lough and Sillees River (Bancroft & Wyse Jackson 1995; Olaloye 1974; Tavener-Smith 1965a, 1965b, 1971, 1973; Wyse Jackson 1988 and herein; Wyse Jackson & Bancroft 1995a).

Order CRYPTOSTOMATA (9)*
- **Hexites paradoxus* sp. nov.
- **Nematopora hibernica* sp. nov.
- **Pseudonematopora planatus* sp. nov.
- **Rhabdomeson progracile* Wyse Jackson & Bancroft
- **R. rhombiferum* (Phillips)
- **Rhombopora cylindrica* sp. nov.
- **R. hexagona* sp. nov.
- **Streblotrypa pectinata* Owen
- **Clausotrypa ramosa* (Owen) comb. nov.

Order TREPOSTOMATA (7)
- **Leioclema indentata* sp. nov.
- **Dyscritella miliaria* (Nicholson)
- **Tabulipora urii* (Fleming)
- **T. howsii* (Nicholson)
- **T. minima* Lee
- **Stenophragmidium* sp.
- †Nodular trepostome

Order CYSTOPORATA (4)
- **Fistulipora incrustans* (Phillips)
- **Goniocladia cellulifera* (Etheridge, jun.)
- †*Goniocladia* sp.
- **Sulcoretepora parallela* (Phillips)

Order FENESTRATA (49)
- **Baculopora megastoma* (M'Coy)
- **Diploporaria marginalis* Young & Young
- **D. tenella* Wyse Jackson
- **Ichthyorachis newenhami* M'Coy
- **Thamniscus colei* Wyse Jackson
- **Rhombocladia dichotoma* (M'Coy) comb. nov.
- *Penniretepora pluma* (Phillips)
- *P. gracilis* (M'Coy)
- *P. frondiformis* Olaloye
- *P. normalis* Olaloye
- *P. cucullea* Olaloye
- *P.* cf. *flexicarinata* Young & Young
- *P. sinuosa* (Hall)
- *P. elegantula* (Etheridge, jun.)
- *P. rotunda* Olaloye
- *P. tortuosa* Olaloye
- *Fenestella frutex* M'Coy
- *F. ivanovi* Shulga-Nesterenko
- *F. multispinosa* Ulrich
- *F. modesta* Ulrich
- *F. hemispherica* M'Coy
- *F. parallela* Hall
- *F. rudis* Ulrich *multinodosa* Tavener-Smith
- *F. plebeia* M'Coy
- *F.* cf. *arthritica* (Phillips)
- *F. praemagna* Shulga-Nesterenko
- *F. fanata* Whidborne *carrickensis* Tavener-Smith
- *F.* cf.*spinacrisata* Moore
- *F.* cf.*funicula* Ulrich
- *F.* cf.*filistriata* Ulrich
- *F. subspeciosa* Shulga-Nesterenko
- *F. pseudovirgosa* Nikiforova
- *F.* cf. *albida* Hall
- *F. oblongata* Koenig
- *F.* cf. *delicatula* Ulrich
- *F. polyporata* (Phillips)
- *F. irregularis* Nekhoroshev
- *Hemitrypa hibernica* M'Coy
- *Levifenestella undecimalis* Shulga-Nesterenko
- *Minilya plummerae* (Moore)
- *M. binodata* (Condra)
- *M. oculata* (M'Coy)
- *Polypora dendroides* M'Coy
- *P. verrucosa* M'Coy
- *P. stenostoma* Tavener-Smith
- *Ptilofenestella carrickensis* Tavener-Smith
- *Ptiloporella varicosa* (M'Coy)
- *Ptylopora pluma* M'Coy *parva* Tavener-Smith
- *Septopora hibernica* Tavener-Smith

* Described in this study; † to be described elsewhere.

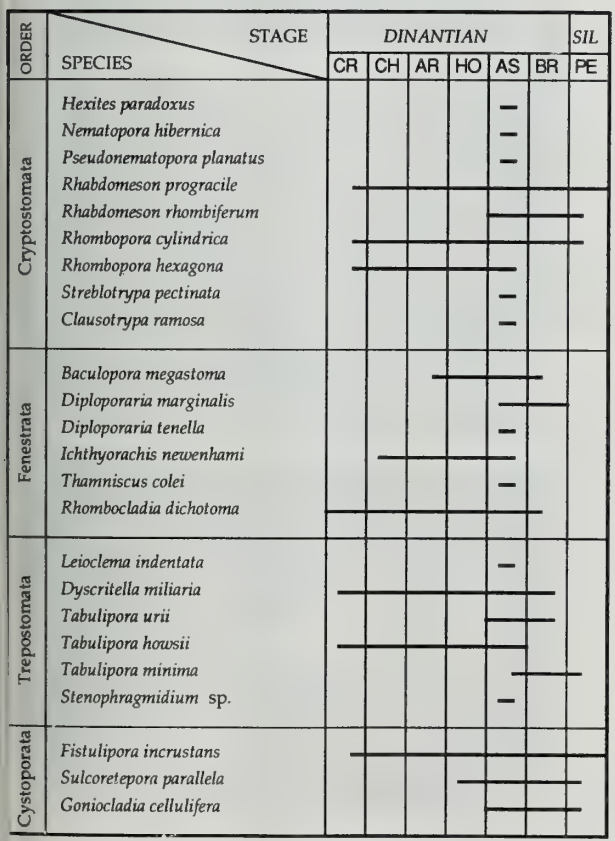
**Table 33** Abundance and diversity of the fauna at Carrick Lough and Sillees River.

| Element | Number of genera* | Number of species* |
|---|---|---|
| Bryozoans | 30 | 69 |
| Brachiopods | 47 | 56 |
| Arthropods | | |
| Trilobites | 6 | 7 |
| Ostracods | 1 | 1 |
| Echinoderms | | |
| Crinoids | 2+ | 2+ |
| Blastoids | 1 | 1 |
| Molluscs | | |
| Gastropods | 4 | 4/5 |
| Bivalves | 2 | ?2 |
| Sponges | ? | ?10 |
| Corals | 3 | ?4 |
| Annelids | 1 | 1 |

*Modified from Brunton (1987)

Although the fauna from County Fermanagh is very well-known, its palaeoecology has been a matter of some debate. The succession at Carrick Lough consists of thin alternating beds of dark argillaceous muddy limestones and paler grey to yellowish bioclastic limestones, while at Sillees River the fauna was etched from biomicritic limestones. The lithology of the bryozoan-bearing strata is that of a distal reef or off-reef deeper water facies.

Extensive reef development occurred in the Asbian of north west Ireland (George *et al.* 1976); one such reef lay just south of the collecting localities which are in proximal reef or off-reef facies (Tavener-Smith 1973).




Abbreviations: SIL: Silesian; CR: Courceyan; CH: Chadian; AR: Arundian; HO: Holkerian; AS: Asbian; BR: Brigantian; PE: Pendleian.

**Fig. 104** Range chart of bryozoans described in this study.

Bryozoans favour clean sediment-free water in which suitable substrates are available (Schopf 1969, Cuffey 1970). The depositional environment at Carrick Lough and Sillees River did not favour extensive bryozoan colonisation because the water was too muddy, as was the substrate. *Fistulipora incrustans* and *Tabulipora howsii* colonised substrates such as brachiopod shells, spines and other bryozoans. They developed small button-like zoaria, which were size-controlled because the adjacent muddy sediment could not be extensively encrusted by bryozoans. Similar evidence for the soft nature of the substrate is suggested by brachiopod attachment styles. The 56 brachiopod species discussed by Brunton, 1987) are more or less equally divided into those that are pedicle supported, quasi-infaunal, and spine supported. Only 3 species were found to be permanently cemented, probably to other brachiopod shells. It is suggested that bryozoans found permanent points of attachment to small shelly substrates from which erect or adnate colonies developed, and that they were not attached directly to any lithic substrate.

Bryozoans are abundant at Carrick Lough and Sillees River, and calcified, decalcified and silicified zoaria have been obtained. Silicification seems to have occurred in the pale limestones and not in the argillaceous and muddy limestones. It is impossible to quantify the abundance of bryozoan colonies in pure numerical values. This is due to the very fragmented nature of the zoaria. Almost without exception all colonies are broken or disarticulated but not heavily abraded nor shredded into fine hash. Bryozoan colonies are found lying on bedding planes and are stacked one upon another.

The fauna comprised bryozoans of four of the five stenolaemate orders (cyclostomes were absent), with a numerical and taxonomic weighting towards the fenestrates. The cryptostome taxa all formed small delicate erect expansions and were quite abundant. In contrast, while the trepostomes are taxonomically moderately diverse they occurred in small numbers. The cystoporates which comprised three taxa were reasonably abundant.

The bryozoan community was dominated by large erect planar and conical fenestrate zoaria, which exploited the seawater up to 20 cm above the substrate. Between *Fenestella s.l.* zoaria grew the smaller fenestellids such as *Baculopora, Diploporaria, Ichthyorachis, Penniretepora* and *Thamniscus*, as well as the delicate cryptostomes, two *Tabulipora* species and the cystoporates *Sulcoretepora* and *Goniocladia.* Colonising the sea floor were *Rhombocladia, Tabulipora, Stenophragmidium* and *Fistulipora.* In addition *Stenophragmidium* grew epiphytically on a soft cylindrically shaped substrate (possibly algae), and *Tabulipora* and *Fistulipora* encrusted brachiopod spines and crinoid ossicles.

Few holdfasts were recovered from this fauna, which is in keeping with other fenestrate-rich faunas (F.K. McKinney pers. comm.). Of those that were found, the majority belong to the cystoporates *Goniocladia cellulifera* and *Sulcoretepora parallela*, with a single holdfast of *Thamniscus colei* being present in the sample.

The attitude and prevalence of fenestellid fronds on bedding planes, the limited abrasion, and lack of holdfasts indicates that the fauna has been translocated. This movement has taken place downslope off reef slopes into deeper water. However, the movement distance cannot have been great as fragemnts display little abraision of fine surface skeletal detail, such as carinal nodes and the superstructure of *Hemitrypa hibernica.*

If, as Brunton (1987) postulates, the Carrick Lough and Sillees River fauna is an *in situ* assemblage then bryozoans preserved in growth position would be expected. As outlined above they are not thus preserved. Tavener-Smith (1973) considers that the Carrick Lough fauna is an accumulated assemblage, that is it has not been

fossilized *in situ*. From the sedimentological and bryozoan evidence this latter interpretation is preferred. However, the possibility that the fauna represents an *in situ* brachipod community into which bryozoans have been washed from adjacent reef slopes cannot be excluded.

## COMPARISON WITH OTHER ASBIAN FAUNAS.

Asbian faunas in the British Isles have received little attention, and many species recorded from County Fermanagh have not been recorded elsewhere. Bancroft (1984) and Wyse Jackson, Bancroft & Somerville (1991) document the faunas of several sites in Britain:

Ashfell Road Cutting, Cumbria [1 cryptostome species / 7–8 fenestrate species / several trepostome species / 2 cystoporate species].

Odin Fissure, Treak Cliff, Derbyshire [1/8/1/1].

Penruddock, Cumbria [1/12/several/2].

Redesdale, Northumberland [1/11/3/1].

Nant-y-Gamar, near Great Ormes Head, north Wales [1/3/5/1]. This fauna is somewhat unusual as it is trepostome-dominated.

Carrick Lough and Sillees River, County Fermanagh [9/49/7/4].

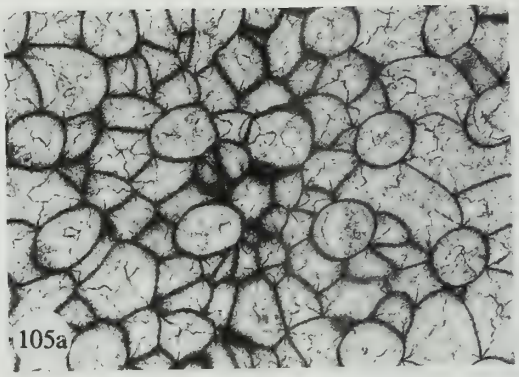
These faunas are generally dominated by fenestrates and fenestellids in particular, with taxa of other bryozoan orders, particularly cryptostomes, being conspicious by their scarcity or apparent absence. This may be due to poor preservation, which makes identification of delicate cryptostome species difficult.

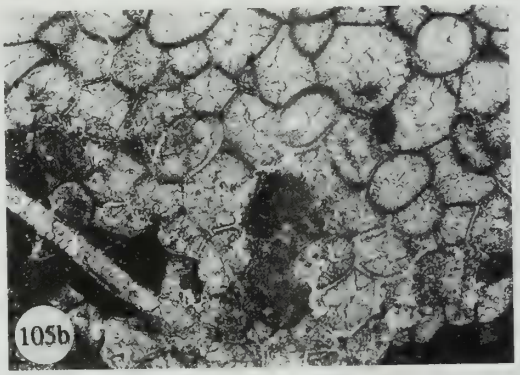
The fauna in County Fermanagh encompasses all species reported from the above localities with the exception of five: *Fenestella matheri, Septopora cestriensis, Batostomella* sp., an undescribed species of *Leioclema*, and *Stenodiscus tumida*. *Fenestella plebeia* is common to all six localities; *Fistulipora incrustans* and *Hemitrypa hibernica* occur in five while *Fenestella bicellulata* occurs in three.

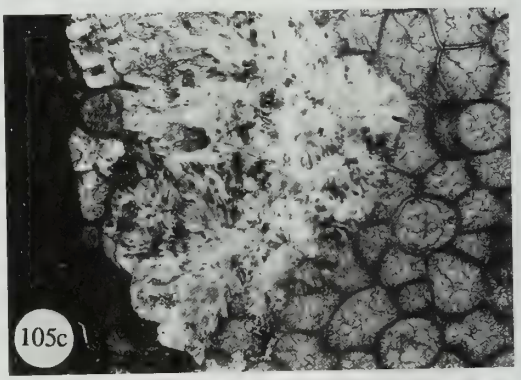
The importance of the Fermanagh fauna lies in its rich taxonomic diversity and reasonable fossil preservation which will allow for future comparison with other Asbian faunas. Such investigations may reveal that the British and Irish faunas are more diverse than hitherto appreciated.

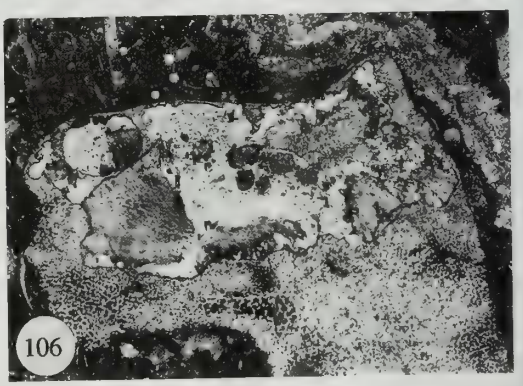
## PATTERNS OF BRYOZOAN ZOARIA REPLACEMENT BY SILICA

Replacement of calcified bryozoan zoaria by silica has allowed for easy extraction from their carbonate matrix by acid digestion. The large number of specimens obtained in this way allows for detailed




**Figs 105, 106** Patterns of silica replacement in bryozoan zoaria from the upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh, as illustrated by examples of *Fistulipora incrustans* colonies; **105,** BMNH PD9740; **105a,** euhedral and sub-hedral microquartz replacement of calcite autozooecial skeletal structure, producing a thin exterior rim that is usually fuzzy in appearance; megaquartz crystals infill the autozooecial chambers, ×25; **105b,** grading of euhedral and sub-hedral microquartz rim into spherulitic chalcedony which replaces the remainder of the skeleton (Pattern 2), ×25; **105c,** total replacement of skeletal walls and autozooecial chamber megaquartz infill by pervasive chalcedony and obliteration of original skeletal structure, ×25; **106,** BMNH PD9741, replacement of crinoid ossicle stereom by radial spherulitic chalcedony; typical Pattern 2 to 3 replacement, ×25.

quantitative taxonomic, ontogenetic and palaeoecological studies. However, it has been argued that the silicification process is selective and does not necessarily preserve all elements of a fauna (Whittington & Evitt 1954), and secondly, that preservation is poor and only retains the external features of the skeleton (Cooper & Grant 1972–1975, Tavener-Smith 1973, Taylor & Curry 1985).

Both calcified and silicified bryozoan fragments are found at Carrick Lough and Sillees River, and comparison of both fractions indicates that more taxa are represented silicified than calcified. This probably reflects the ease by which silicified specimens are retrieved. Some authors report excellent preservation by silica of invertebrate skeletal microstructure (Brunton 1976, Holdaway & Clayton 1982), and of plant vessels (Stein 1982), while Schmitt & Boyd (1981) noted that relict ultrastructure is commonly observed in megaquartz crystals. There is no doubt that the process of silicification can produce both excellent and poor preservation. Schmitt & Boyd (1981) noted that the quality of preservation is related to the timing of replacement: poor preservation is due to delayed replacement, whereas excellently preserved fine detail is produced by immediate replacement of the calcite skeleton by silica. They sub-divided silica patterns into five major types, of which patterns 1 to 4 represent delayed replacement and pattern 5 immediate replacement.

A number of randomly orientated thin sections were cut from silicified blocks collected from Carrick Lough. In general bryozoan autozooecial chambers are infilled with megaquartz, whereas the skeleton is replaced by a mixture of spherulitic chalcedony which is radial in appearance, tiny sub-hedral to euhedral microquartz crystals (<20um), and occasionally some megaquartz.

Silicification may occur in descrete steps, which will produce different silica styles. Initially the calcite bryozoan zoarium is quite faithfully replaced by euhedral and sub-hedral microquartz crystals, producing a thin exterior rim that is usually fuzzy in appearance (Fig. 105a). As the intensity of silicification increases autozooecial and vesicular chamber walls are totally replaced by spherulitic chalcedony (Pattern 2 of Schmitt & Boyd 1981) (Fig. 105b). Finally, chalcedony pervades both the walls and the megaquartz crystals that infilled autozooecial chambers obliterating all original skeletal structure (Fig. 105c). Overgrowing this ubiquitious chalcedony are found small rhombic dolomite crystals. In some zoaria silicification has not been totally pervasive. Where this occurs the outer laminated skeleton (eg. in *Fenestella s.l.*) is replaced, with the inner granular tissue left unaltered.

These silica patterns indicate that replacement of the bryozoan colonies in County Fermanagh was delayed. In many cases replacement is incomplete: colonies may be lightly silicified on their outer surfaces and not silicified internally, or else portions of branches may be silicified and others not. In these situations colonies are very delicate and easily fragmented. Rarely are zoaria completely silicified. However, where this has occurred, considerable skeletal detail is retained, which allows for reasonable taxonomic determinations and morphological descriptions. In these cases the silica style is that of Pattern 2.

## KEY TO THE IDENTIFICATION OF SOME LOWER CARBONIFEROUS BRYOZOA

In total 29 genera, containing 68 species have been described from the Viséan of County Fermanagh. This key is an aid to their identification. It has been necessary to construct the key in two styles: a multi-element dichotomous-trichotomous portion and a tabular portion. Where possible taxa are keyed out in the former, but where there are a large number of species in a genus (as with *Fenestella s.l.*) the latter has been used. In some cases several routes through the key will lead to the same taxon. No attempt has been made to designate the various *Fenestella* species to the genera erected by Morozova (1974).

The key to *Fenestella s.l.* species and other fenestrate taxa is based on the findings of Bancroft (1984), Olaloye (1974), and Tavener-Smith (1965a, 1965b, 1971, 1973). No attempt has been made to check their taxonomic determinations.

### Key

1 Autozooecia developed on obverse surface only, tripartite skeleton developed ..... 2
Autozooecia developed throughout zoarium ..... 26

2 Zoaria reticulate ..... 3
Zoaria small pinnate or non-pinnate expansions ..... 12
Zoaria basket or cup-shaped ..... 25

3 2 rows of autozooecia on branches ..... 4
More than two rows of autozooecia developed ..... 11

4 Branches all the same size ..... 5
Branches of two sizes: a few primary and many secondary ..... ***Ptiloporella varicosa***

5 Median carina present ..... 6
Median carina absent ..... ***Levifenestella undecimalis***

6 Obverse surface protected by a honeycomb-like superstructure ..... ***Hemitrypa hibernica***
Obverse surface not covered by a superstructure ..... 7

7 Carinal nodes arranged in a straight line *Fenestella* s.l. (go to Table 34)
Carinal nodes in two offset zigzag rows ..... 8

8 Fenestrules quadrate, hourglass-shaped, serving four autozooecial apertures ..... 9
Fenestrules elongate, serving 8 autozooecial apertures ..... 10

9 Peristomes large, median carina well developed, reverse surface often nodulose ..... ***Minilya plummerae***
Peristomes slight, median carina weak, reverse surface smooth to marginally striated ..... ***Minilya nodulosa***

10 Branch margins slightly indented by autozooecial apertures, median carina weak, one carinal node situated at branch/dissepiment junction ..... ***Minilya binodata***
Branch margins straight, median carina moderate, arrangement of carinal nodes somewhat irregular ..... ***Minilya oculata***

11 3 rows of autozooecia, keyhole-shaped apertures ..... ***Polypora stenostomata***
4–5 rows of autozooecia, oval apertures, fenestrules oval 2.50mm long ..... ***Polypora dendroides***
4 rows of autozooecia, peristomes around apertures, fenestrules elongate 3.30–4.70mm long ..... ***Polypora verrucosa***

12 Zoarium pinnate ..... 13
Zoarium non-pinnate ..... 21

13 Lateral branches lack dissepiments ..... 14
Lateral branches connected with dissepiments ..... ***Ptylopora pluma parva***
Lateral branches coalesce ..... ***Septopora hibernica***

14 2 rows of autozooecia on branches ..... 15
More than two rows of autozooecia ..... ***Ichthyorachis newenhami***

15 1 autozooecial aperture between lateral branches ..... 16
2 autozooecial apertures between lateral branches ..... 18
>5 autozooecial apertures between lateral branches ..... ***Penniretepora tortuosa***

16 Lateral branches straight ..... 17
Lateral branches sinuous (margins broken by protruding autozooecial apertures) ..... ***Penniretepora gracilis***

17 Median carina strong, straight ..... ***Penniretepora frondiformis***
Median carina weak, straight ..... ***Penniretepora normalis***
Median carina consists of 3 sinuous pustulose ridges ..... ***Penniretepora flexicarinata***

18 Main stem straight ..... 19
Main stem sinuous ..... ***Pennitepora elegantula***

19 Lateral branches straight ..... 20
Lateral branches sinuous ..... ***Pennitepora cucullea***

20 Peristomes, horseshoe-shaped, developed on distal side of autozooecial apertures ..... ***Pennitepora pluma***
Peristomes absent ..... ***Pennitepora sinuosa***

21 2 rows of autozooecia on branches ..... 22
More than two rows of autozooecia on branches ..... 23

22 Lateral margins of branches serrated ..... ***Diploporaria marginalis***
Lateral margins flexuous or smooth ..... ***Diploporaria tenella***

23 Branches delicate, flexuous, oval/circular apertures ..... ***Baculopora megastoma***
Branches robust, apertures with peristomes ..... 24

24 Complete peristomes surround apertures ..... ***Thamniscus colei***
Proximal peristomes only ..... ***Thamniscus rankin***

25 Branches connected by dissepiments ..... ***Ptilofenestella carrickensis***
Branches bear no dissepiments ..... ***Thamniscus colei***

26 Zoaria ramose or encrusting, with polymorphic zooecia, distinct endozonal and exozonal differentiation ..... 27
Zoaria possess cystopores ..... 32

Zoaria dendroid with zooecia budded from central axis ..... 34
27 Mesozooecia developed ..... 28
Exilazooecia developed ..... 29

28 Zoaria ramose with thick exozone and autozooecia heavily indented by acanthostyles ..... ***Leioclema indentata***

29 Exilazooecia common with many disposed between autozooecia ..... ***Dyscritella miliaria***
Exilazooecia relatively rare ..... 30
30 Ring septa developed ..... 31
Hemiphragma developed ..... ***Stenophragmidium*** sp

31 Zoaria ramose, autozooecial apertures circular, ring septa tips slightly thickened, deflected proximally, exilazooecia in clusters ..... ***Tabulipora urii***

Zoaria thin adnate sheets, autozooecial apertures polygonal, ring septa planar/thin, exilazooecia rare ..... ***Tabulipora howsii***
Zoaria robust, exozone thin, autozooecial apertures oval, exilazooecia rare ..... ***Tabulipora minima***

32 Zoaria encrusting, adnate, with well developed rectangular (vesicles) cystopores between tubular autozooecia ..... ***Fistulipora incrustans***
Branches bifoliate with spherical cystopores ..... 33

33 Branches strap-like, zoaria budded from a plicated median wall, autozooecial apertures with proximal lunaria ..... ***Sulcoretepora parallela***
Branches sub-rounded, with a distinct keel and carina, autozooecia budded from a straight median wall ..... ***Goniocladia cellulifera***

34 Branches articulated, very slender (01–25mm), circular or polygonal in cross-section, hemisepta absent ..... 35
Branches not articulated, cylindrical (05–60mm), hemisepta usually present in pairs ..... 37

35 Autozooecial apertures present on all branch surfaces ..... 36
Autozooecial apertures absent from a distinct reverse surface ..... ***Nematopora hibernica***

36 Branch cross-section polygonal, autozooecia budded in annular fashion, autozooecial apertures oval, separated from each other by longitudinal ridges ..... ***Hexites paradoxus***
Branch cross-section circular, autozooecial budding radial, autozooecial apertures circular, with proximal peristomes ..... ***Pseudonematopora planatus***

37 Metapores very common, arranged in linear rows in interapertural areas ..... ***Streblotrypa pectinata***
Metapores irregularly disposed in interapertural areas ..... ***Clausotrypa ramosa***
Metapores either absent or only 1 per autozooecium ..... 38

38 Central axial cylinder present ..... 39
Axial cylinder not present ..... 40

39 Autozooecial apertures oval, of constant dimensions, with a large acanthostyle situated proximally, smaller stylets may be present ..... ***Rhabdomeson progracile***
Autozooecial apertures pyriform, distally flared, of varying dimensions, over 20 small stylets developed around apertures ..... ***Rhabdomeson rhombiferum***

40 Autozooecial apertures circular, of constant size, with acanthostyles and heterostyles disposed in a circle around them, a single metapore may be situated proximal to autozooecia ..... ***Rhombopora cylindrica***
Autozooecial apertures circular to oval, of varying size around zoarium with heterostyles arranged in a hexagonal pattern ..... ***Rhombopora hexagona***

**Table 34** Tabular key for the identification of *Fenestella* species from the Viséan of County Fermanagh and from other localities in the British Isles [* = not recorded from Carrick Lough by Tavener-Smith (1973)].

| SPECIES \ CHARACTER | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Fenestella bicellulata* * | A | A | A | A | A | B | A | F | A | A | A | C | A | A | C | B | B | D |
| *Fenestella ivanovi* | A | B | A | A | B | A | A | C | B | A | A | C | B | A | C | B | A | A |
| *Fenestella frutex* | A | B | A | F | B | A | A | B | B | A | A | A | A | A | C | A | B | A |
| *Fenestella multispinosa* | A | B | A | A | B | B | A | E | C | A | A | C | B | A | C | A | B | A |
| *Fenestella tuberculo-carinata* * | A | B | B | A | B | B | A | G | A | A | A | B | A | C | D | B | A | A |
| *Fenestella plebeia* | A | C | B | C | B | A | A | B | A | A | A | A | B | A | D | B | B | A |
| *Fenestella papilliata* * | A | C | B | G | C | B | A | G | C | A | ? | C | A | C | C | B | A | B |
| *Fenestella morrisii* * | A | C | ? | E | ? | B | C | A | A | A | ? | ? | ? | ? | ? | A | B | ? |
| *Fenestella polyporata* | B | D | D | I | D | B | A | F | A | A | A | C | C | A | C | A | B | C |
| *Fenestella quadridecimalis* * | B | E | D | I | C | B | B | G | C | A | C | B | D | A | A | B | B | B |
| *Fenestella modesta* | A | B | B | B | B | A | A | B | C | A | C | D | A | A | C | B | B | A |
| *Fenestella hemispherica* | A | B | B | B | B | B | ? | F | A | A | B | C | D | B | B | B | A | B |
| *Fenestella parallela* | A | B | B | B | B | B | ? | B | C | B | C | D | B | D | A | A | B | A |
| *Fenestella rudis multinodosa* | A | B | B | B | B | B | A | G | A | B | C | D | E | A | D | B | A | A |
| *Fenestella* cf. *arthritica* | C | C | C | C | C | B | A | F | A | A | A | A | C | C | C | B | B | B |
| *Fenestella praemagna* | C | C | B | H | C | B | B | F | C | A | A | A | C | C | C | B | A | B |
| *Fenestella fanata carrickensis* | A | C | C | B | C | B | A | G | A | C | C | C | C | B | B | A | A | B |
| *Fenestella* cf. *spinacrista* | A | C | C | G | B | B | A | B | A | A | A | C | B | A | C | B | B | B |
| *Fenestella* cf. *filistrata* | D | C | C | D | B | B | A | G | C | C | C | D | E | A | C | A | A | A |
| *Fenestella* cf. *funicula* | A | C | C | C | C | B | A | E | A | A | A | A | C | A | D | B | B | A |
| *Fenestella subspeciosa* | B | C | B | G | C | B | B | E | C | B | B | C | E | B | D | B | B | A |
| *Fenestella* cf. *albida* | B | C | C | D | C | B | B | F | B | A | A | D | E | C | C | B | A | B |
| *Fenestella oblongata* | B | D | C | E | C | B | A | B | A | C | C | A | D | A | B | B | B | D |
| *Fenestella* cf. *deliculata* | A | D | C | E | B | B | A | E | A | A | A | D | C | A | D | B | A | B |
| *Fenestella irregularis* | B | E | D | I | C | B | A | B | A | B | C | C | E | C | C | B | B | A |
| *Fenestella pseudovirgosa* | B | C | D | H | C | B | A | F | A | A | A | A | D | A | A | B | B | C |

Explanation of characterers used in Table 34:

1. Branch shape:
   A, Straight; B, Sinuous; C, Irregular; D, Partly straight partly sinuous
2. Fenestrule length:
   A, < 0.5 mm; B, 0.5–1.0 mm; C, 1.0–2.0 mm; D, 2.0–3.0 mm; E, > 3.0 mm
3. Fenestrule width:
   A, < 0.5 mm; B, 0.5–0.75 mm; C, 0.75–1.0 mm; D, > 1.0 mm
4. Number of autozooecial apertures per fenestrule:
   A, 2; B, 3; C, 4; D, 5; E, 5–8; F, 2–3; G, 3–4; H, 4–5; I, > 8
5. Interapertural distance:
   A, < 0.2 mm; B, 0.2–0.3 mm; C, > 0.3 mm
6. Zooecial aperture/branch/dissepiment relationship:
   A, Aperture occurs at branch/dissepiment junction; B, Apertures situated anywhere along branch length
7. Zoarial appearance:
   A, Rigid; B, Lax; C, High angle cone
8. Fenestrule shape:
   A, Square; B, Rectangular; C, Hour-glass; E, Various; F, Elongate-rectangular; G, Elongate-oval
9. Fenestrule edges:
   A, Straight; B, Indented (by peristomes), C, Slightly undulating
10. Carina:
    A, Distinct; B, Indistinct; C, Absent
11. Inclination of branch sides from carina:
    A, Steep; B, moderate; C, Gentle
12. Carinal nodes:
    A, Large; B, Moderate; C, Small; D, Poorly developed
13. Spacing of carinal nodes:
    A. Regular – close < 0.25 mm; B, Regular – moderate 0.25 – 0.50 mm;

C, Regular – wide 0.50 – 1.00 mm; D, Regular – very wide > 1.00 mm; E, Irregular

14. Dissepiment depression on obverse surface:
A, Well; B, Moderate; C, Slight; D. None (flush with branch surface – indicative of *Fenestella parallela)*
15. Dissepiment depression on reverse surface:
A, Well; B, Moderate; C, Slight; D, None (flush with branch surface)
16. Incipient 3rd row of zooecial chambers developed before bifurcation:
A, Present; B, Absent
17. Extra zooecial chamber in angle of bifurcation:
A, Present; B, Absent
18. Rib(s) on dissepiment obverse surface:
A, Present; B, Absent; C, Present (extending to meet carina); D, Occasionally present

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